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Lake nutrient stoichiometry is less predictable than nutrient concentrations at regional and sub-continental scales

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Abstract. Production in many ecosystems is co-limited by multiple elements. While a known suite of drivers associated with nutrient sources, nutrient transport, and internal processing controls concentrations of phosphorus (P) and nitrogen (N) in lakes, much less is known about whether the drivers of single nutrient concentrations can also explain spatial or temporal variation in lake N:P stoichiometry. Predicting stoichiometry might be more complex than predicting concentrations of individual elements because some drivers have similar relationships with N and P, leading to a weak relationship with their ratio. Further, the dominant controls on elemental concentrations likely vary across regions, resulting in context dependent relationships between drivers, lake nutrients and their ratios. Here, we examine whether known drivers of N and P concentrations can explain variation in N:P stoichiometry, and whether explaining variation in stoichiometry differs across regions. We examined drivers of N:P in ~2,700 lakes at a sub-continental scale and two large regions nested within the sub-continental study area that have contrasting ecological context, including differences in the dominant type of land cover (agriculture vs. forest). At the sub-continental scale, lake nutrient concentrations were correlated with nutrient loading and lake internal processing, but stoichiometry was only weakly correlated to drivers of lake nutrients. At the regional scale, drivers that explained variation in nutrients and stoichiometry differed between regions. In the Midwestern U.S. region, dominated by agricultural land use, lake depth and the percentage of row crop agriculture were strong predictors of stoichiometry because only phosphorus was related to lake depth and only nitrogen was related to the percentage of row crop agriculture. In contrast, all drivers were related to N and P in similar ways in the Northeastern U.S. region, leading to weak relationships between drivers and stoichiometry. Our results suggest ecological context mediates controls on lake nutrients and stoichiometry. Predicting stoichiometry was generally more difficult than predicting nutrient concentrations, but human activity may decouple N and P, leading to better prediction of N:P stoichiometry in regions with high anthropogenic activity.

Key words: LAGOS database; lake nutrients; land use; landscape limnology; nitrogen; nutrient loading concept; phosphorus; stoichiometry.

Introduction

Absolute concentrations of a limiting nutrient play a central role in ecosystem dynamics, but the relative availability of some nutrients, or stoichiometric ratios, also affect a range of ecological patterns and processes (Sterner and Elser 2002). Nutrient co-limitation by nitrogen (N) and phosphorus (P) is pervasive across a range of terrestrial, aquatic, and marine ecosystems (Elser et al. 2007, Harpole et al. 2011, Paerl et al. 2016), suggesting that multiple elements should be considered in studies of ecosystem production. Elemental ratios can also influence a range of ecological processes (Sardans et al. 2011), including community composition (Tilman et al. 1982, Poxleitner et al. 2016), likelihood of toxin-producing algal blooms (Davidson et al. 2012, Michalak et al. 2013), trophic interactions (Frost et al. 2005), and interspecific competition (Hall 2004). The influence of N:P stoichiometry on a range of ecological phenomena, coupled with the reality that anthropogenic activities are shifting the balance of elements (Peñuelas et al. 2011, 2013), underscore the need to examine drivers of variability in both N and P over space.

Many previous studies have identified drivers of nutrient concentrations or cycles at broad regional to continental spatial extents (Jobbagy and Jackson 2001,

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Booth et al. 2005, Taranu and Gregory-Eaves 2008, Read et al. 2015, Liu et al. 2016), yet few have done the same for nutrient ratios (but see Arbuckle and Downing 2001, Hessen et al. 2009, Elser et al. 2009, Dijkstra et al. 2012, He et al. 2014, Martyniuk et al. 2016). Predicting nutrient ratios is likely challenging, as illustrated by a simple heuristic example of scenarios for predicting ratios and the individual elements that comprise them (Fig. 1A). We expect that ratios may be related to drivers if one nutrient responds strongly to a driver but the other is unaffected (single nutrient response). In contrast, if both nutrients respond similarly to a driver, ratios would remain constant (parallel nutrient response). In principle, prior knowledge on whether the major drivers of N and P vary across space should inform patterns of nutrient stoichiometry, but that remains largely unknown.

Predicting stoichiometry across increasingly broad, heterogeneous spatial scales poses additional challenges due to context dependency. Context dependency leads to differences in a wide range of ecological relationships across space and time, making it difficult to generalize results across regions (e.g., Heino et al. 2011, Ricciardi et al. 2013). The strength of driver–response relationships could be qualitatively inconsistent over broad spatial scales due to nonlinear relationships between drivers

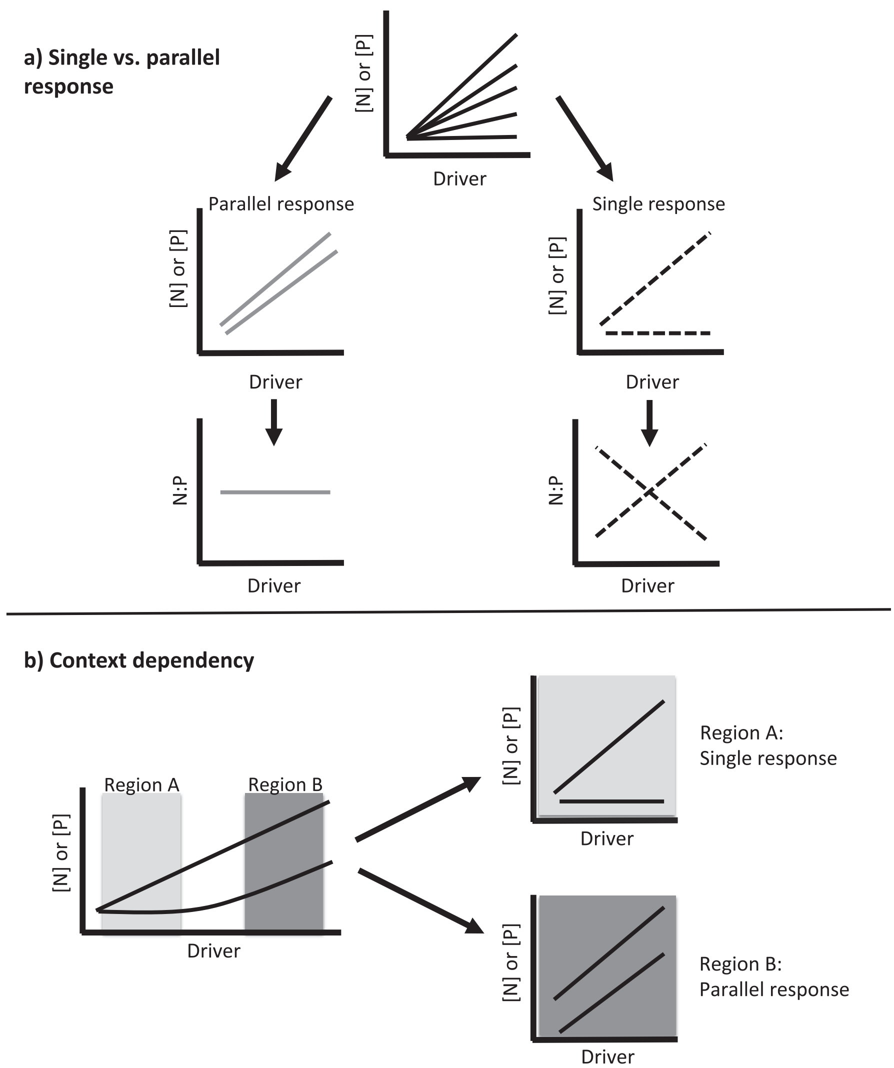

Fig. 1. Conceptual scheme for predicting stoichiometry of two nutrients. (A) Nutrients are related to environmental drivers in different ways, and two nutrients (e.g., N and P) may or may not relate to the driver in a similar way. Similar relationships for both nutrients would lead to a parallel response (left side, gray lines) while different relationships for each nutrient would lead to a single response (right side, dashed lines). Whether a response is single or parallel should determine whether a driver can be used to predict stoichiometry, with parallel responses leading to weak prediction of stoichiometry and single responses leading to strong prediction of stoichiometry. (B) Nonlinear relationships between drivers and nutrients may lead to differences in regions with different environmental context. Region A (light gray) has relatively low values of the driver variable, and we observe a single nutrient response, while in Region B (dark gray) has relatively high values of the driver variable and we observe a relatively parallel response.

and responses (Fig. 1B). Context dependency is often the product of multiple ecological characteristics acting at different scales, sometimes in complex ways. For example, wetlands are known to act as a sink for phosphorus in watersheds, but they can also act as a source of phosphorus when there is a low percentage of agriculture in the basin (Fergus et al. 2011). Because context dependency is likely to cause difficulty in generalizing the drivers of any single nutrient over space or time, it may affect multiple nutrients in different ways, compounding the challenges for predicting stoichiometric ratios. Here, we evaluate whether explaining variation in stoichiometry is actually more difficult than it is for nutrient ratios and explicitly consider the effects of context dependency by contrasting results from a broad, heterogeneous, sub-continental spatial extent to two regions with more homogenous characteristics.

We investigated these ideas using data from lake ecosystems because N and P are key nutrients and there are well-established drivers of N and P concentrations that have been identified over the past several decades (Edmondson 1961, Vollenweider 1975, Taranu and Gregory-Eaves 2008, Knoll et al. 2015, Read et al. 2015, Soranno et al. 2015*b*). The nutrient-loading concept (reviewed by Brett and Benjamin 2008) provides a framework for predicting single nutrients in lakes based on drivers that are organized into three categories: sources, transport, and in-lake processing of nutrients. Most research has focused on P as a primary limiting nutrient in lakes, but the same drivers are also effective for predicting concentrations of N at broad scales (Bachmann 1984, Read et al. 2015). More recently, N:P stoichiometry has also been related to drivers that are known to influence single nutrients, including N deposition (Elser et al. 2009, Hessen et al. 2009, Crowley et al. 2012), agricultural land use (Arbuckle and Downing 2001, Vanni et al. 2011), climate (Chen et al. 2015), and the extent of human impact in a study region (Yan et al. 2016).

Our overall goal was to identify drivers of lake N:P stoichiometry over space and to determine how they differ across regions with different ecological contexts. We used the LAke GeOSpatial and temporal database (LAGOS, Soranno et al. 2015*a*), a sub-continental scale database with recent N and P data for ~2,700 lakes and a comprehensive suite of drivers related to nutrient loading and processing, to identify drivers of stoichiometry and to create a strong contrast between regions to evaluate the role of context dependency in predicting nutrients and their ratios. First, we evaluated how explaining variation in N:P ratios compares to explaining variation in single nutrient concentrations. We expected that N:P stoichiometry should only be predictable if drivers have contrasting effects on N and P. Alternatively, if all drivers were related to N and P in similar ways, we expected weak relationships between drivers and stoichiometry. We examined these relationships at a sub-continental scale, and also created two sub-regions within the study area that represented a strong contrast in ecological context. The two regions differed in their dominant land use/land cover (agricultural vs. forested), and amounts of topographical relief, runoff, precipitation, and atmospheric nitrogen deposition. Comparing models for those two regions allowed us to evaluate how explaining variation in stoichiometry was influenced by context; we expected to observe differences in models for regions with very different underlying environmental characteristics and levels of human impact.

Methods

Study lakes

We conducted our analysis on epilimnetic nutrient data and geospatial data from the LAGOS database, including nutrient data from LAGOS-NE$_{LIMNO}$ v. 1.054.1 and landscape and lake feature data from LAGOS-NE$_{GEO}$ v. 1.03, (for details, see Soranno et al. 2015*a*). Briefly, LAGOS-NE$_{LIMNO}$ includes nutrient data from 54 agency, university, and citizen monitoring data sets, and LAGOS-NE$_{GEO}$ includes geospatial data on climate, hydrology, geology, and land use/land cover of lakes that are derived at multiple spatial extents. The nutrient and geospatial data in LAGOS-NE cover approximately 1,800,000 km^2 over a 17-state region in the Midwestern and Northeastern United States. We limited our analysis to epilimnetic nutrient data from 2,687 lakes that had concurrent observations of total nitrogen (TN) and total phosphorus (TP) during the summer stratified season (15 June–15 September) in the most recent decade of data in the database (2002–2011). Most lakes had multiple observations during that time period; we used the median nutrient concentration and median N:P ratio for each lake in our analysis.

Within the LAGOS-NE$_{GEO}$ database, we identified variables that characterize nutrient sources, transport, and internal processing. Some types of data, including watershed land use, lake depth, watershed area and lake area (used to approximate residence time), were available for each individual lake and watershed, while others, including climate, hydrology, and deposition data, were only available for fine-scale hydrologic unit code (HUC) 12 watershed units (~20,000 HUC 12 watersheds exist within the data set that are nested within larger watersheds in the HUC classification system). Approximately 30% of HUC 12 watersheds included more than one lake that was included in our analysis, but never more than nine lakes in the same HUC 12, and over 80% of HUC 12s included three or fewer lakes, so most lakes have unique values for each driver. While our final models included either individual watershed or HUC 12 scale data for predictors, we also tested whether regional-level (HUC 4 watershed) predictor data were important in preliminary models. We did not include HUC 4 regional predictors because they were redundant with the local-scale data for the same predictors. Specific nutrient source, transport, and internal processing variables are

Table 1. Driver and response variables used in the analysis.

Variables	Northeastern	Sub-continental	Midwestern
Nutrient sources			
Pasture agriculture (%)	2.99	11.9	9.14
Row crop agriculture (%)	1.55	30.0	67.9
Urban land use (%)	8.89	9.18	8.15
Forest land use (%)	64.4	34.2	7.02
N deposition, 2005 data (kg nitrate/ha)	3.57	4.87	5.5
Nutrient transport			
Precipitation, 30-yr normal (mm)	1,179	977	868
Baseflow (%)	51.1	43.2	39.6
Internal processing			
Maximum depth (m)	9.75	8.53	6.71
Residence time (WA:LA)	8.06	11.5	19.5
Temperature, 30-yr normal (°C)	6.41	8.83	9.17
TN			
Mean and SD (μg/L)	354 (270)	885 (984)	2,481 (2,139)
Range (μg/L)	98–4,022	55–12,650	278–12,647
TP			
Mean and SD (μg/L)	13.8 (19.1)	42.0 (77.4)	136 (144)
Range (μg/L)	1–199	1–1,455	8.5–1,041
TN:TP (molar)			
Mean and SD	77.2 (38.7)	88.7 (82.8)	80.0 (96.8)
Range	8.0–517	4.7–865	5.7–565

Notes: Watershed area to lake area ratio (WA:LA) and lake depth represent the mean value of all lakes used in analysis. All other metrics are HUC 4 means weighted by area of the HUC 4 watershed. We used WA:LA to approximate residence time.

detailed in Table 1. We placed each driver into a single category that was considered its dominant mechanism for affecting lake nutrients (Table 1), but recognize that some may be associated with one or more subcategories.

Study area

Within the sub-continental data set that encompasses the entire LAGOS study area, we delineated two contiguous regions with contrasting ecological context: one in the Midwestern United States that is predominantly agricultural (hereafter "Midwestern region") and one in the Northeastern United States that is mostly forested (hereafter "Northeastern region"). We used the clear gradient of agricultural and forested land use in the sub-continental study area to create two regions that represent extremes in ecological context because agriculture is clearly related to nutrient inputs to freshwaters (e.g., Carpenter et al. 1998, Smith 2003). The regions, however, also captured gradients in broad-scale nutrient source and transport variables that characterized their ecological context (Fig. 1, Table 1). To create the regions, we aggregated regional (HUC 4) watersheds into larger regions by examining spatial patterns in HUC 4 regional-scale agriculture and combining adjacent HUC 4 watersheds with similar characteristics. The sub-continental extent includes 65 HUC 4 watersheds. For the Northeastern region, we combined 10 adjacent HUC 4 watersheds that had extremely low agricultural land use (<10%), which included 562 lakes with nutrient data. In the Midwestern United States, HUC 4 watersheds all had relatively high agriculture (>50%). We used 75% regional agriculture as a threshold for inclusion within the Midwestern region because that was the regional agriculture threshold where individual lake watersheds within the regional watersheds were predominantly agricultural, rather than a mix of low and high agriculture. We combined seven adjacent HUC 4 watersheds to create the Midwestern region, which included 179 lakes with nutrient data. The Northeastern and Midwestern regions were each spatially contiguous (Fig. 2a).

Statistical analysis

We used partial least squares (PLS) regression to determine which drivers were related to lake nutrients and stoichiometry at the sub-continental spatial extent as well as in each of the two regions. Partial least squares regression is an extension of multiple linear regression where predictors may be colinear, and both predictor and response variables are projected into new spaces (i.e., related to each other; Carrascal et al. 2009). In addition, multiple response variables can be included in the same PLS model. One disadvantage of PLS regression is that it does not account for the hierarchical structure of the data, where lakes are nested within ecological regions. To assess the sensitivity of our inferences to ignoring this spatial structure, we compared PLS regression to a mixed modeling approach that explicitly accounted for the hierarchical data structure. Results of this comparison showed that the two approaches

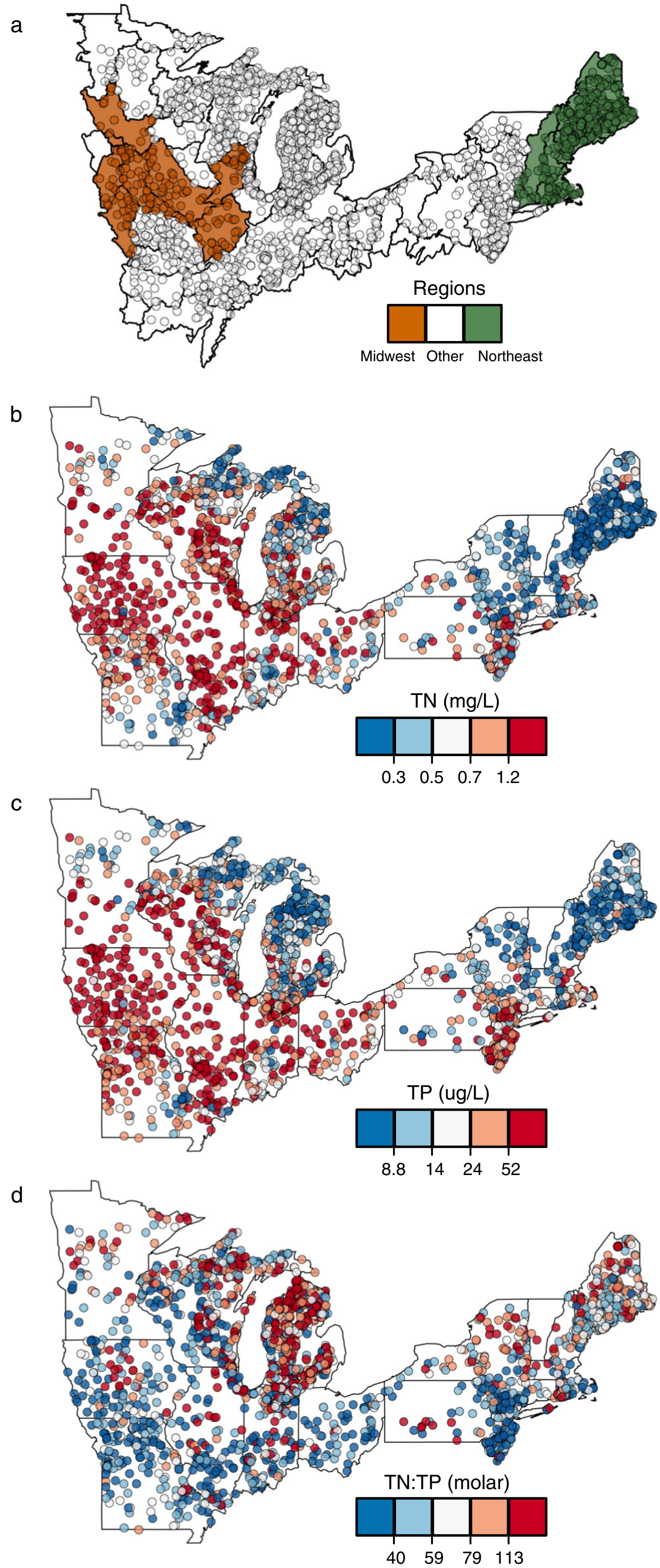

FIG. 2. Quantile maps of (a) the location of lakes included in the Midwestern (orange) and Northeastern (green) regions, (b) TN, (c) TP, and (d) TN:TP. Points represent individual lakes and black lines in panel a represent HUC 4 watersheds.

produced very similar results, suggesting that our inferences and interpretation of the results would be the same with either PLS regression of a mixed model. We created PLS regression models with the three response variables (N, P, N:P) fit simultaneously in three separate models for each of the study areas: the sub-continental extent, Midwestern region, and Northeastern region. We used the plsreg2 function in the plsdepot package (Sanchez 2012) in R (R Core Team 2016). Results from this approach were similar to results from separate PLS models for each response variable.

We compared models using several metrics. First, we used the Variable Importance for Projection (VIP) to show the relative importance for each predictor variable in the projection of the three response variables in two-dimensions (Mehmood et al. 2012). Generally, VIP scores above 1.0 suggest that a variable is important (Fraterrigo and Downing 2008, Mehmood et al. 2012), but variables with scores slightly below 1.0 might be marginally important (Lopez et al. 2008, Monk et al. 2013). Second, we used R^2 as an estimate of the variance explained by the models. Finally, we used the standardized regression coefficients for each predictor and response variable combination, which allowed us to compare the magnitude and direction of the effects of drivers on each response (N, P, N:P) separately.

Results

Nutrient concentrations and stoichiometry at regional and sub-continental extents

Median nutrient concentrations and atomic ratios varied greatly across the sub-continental study extent, from 55 to 12,650 μg/L for TN, 1–1,455 μg/L for TP, and an atomic ratio of 5–865 for TN:TP (Fig. 2, Table 1). There were strong spatial patterns in N and P concentrations, with higher concentrations in most of the Midwestern U.S. and lower concentrations in the Northeastern U.S. and most northern parts of the Midwestern US (Fig. 2b, c). Those spatial gradients resulted in different nutrient concentrations across our two study regions, with high N and P in the Midwestern region and low N and P in the Northeastern region (Table 1). In contrast, the spatial pattern in N:P stoichiometry was much weaker. N:P ratios were generally higher in the northern portion of the sub-continental study extent (Fig. 2d), but estimates of mean N:P and variability in N:P were comparable in the sub-continental extent and each of the two regions (Table 1).

Explaining variation in nutrient concentrations vs. stoichiometry

For all three models, the driver variables explained about half of the variation in N and P concentrations (R^2 range 0.46–0.60), but much less variation in N:P ratios (R^2 range 0.14–0.40). Explanatory power varied across the three models; for both the sub-continental extent and the Northeastern region, drivers explained more variance in nutrient concentrations than stoichiometry, but in the Midwestern region, the R^2 for N:P stoichiometry was closer to R^2 for N and P (Fig. 3). These differences can be explained by how the driver variables are related to nutrients vs. stoichiometry. Generally, effect sizes for driver variables were mostly larger for nutrient concentrations than they were for stoichiometry (Fig. 4), indicating a stronger effect of drivers on nutrient concentrations compared to ratios. Drivers that had different effects sizes for N and P were the only drivers with strong effect sizes for N:P. We describe these results in detail in the following section.

Drivers of nutrients concentration and stoichiometry across ecological context and scale

Nutrient concentrations were related to drivers in all categories of the nutrient loading concept (Table 2), but the identity of important drivers varied across spatial scale and ecological context. At the sub-continental extent, nutrient sources were more strongly related to N, while transport and internal processing drivers were more strongly related to P (Fig. 4a). At the sub-continental scale, VIP scores suggest that nutrient concentrations and ratios are controlled by all types of drivers, while at the regional scale, they are mostly associated with internal processing drivers and a limited number of source variables (Table 2). Nutrient sources (row crop agriculture and forest), nutrient transport (baseflow), and internal processing (lake depth, residence time, and temperature) all had high VIP scores (>1.0) in the sub-continental model. Pasture agriculture had a marginally high VIP score and could also be important. In contrast, a more limited set of drivers were important for each regional-scale model. In the Northeastern region model, two internal processing variables (lake depth and temperature) and one related to nutrient source (forest land use) were important, with marginally important

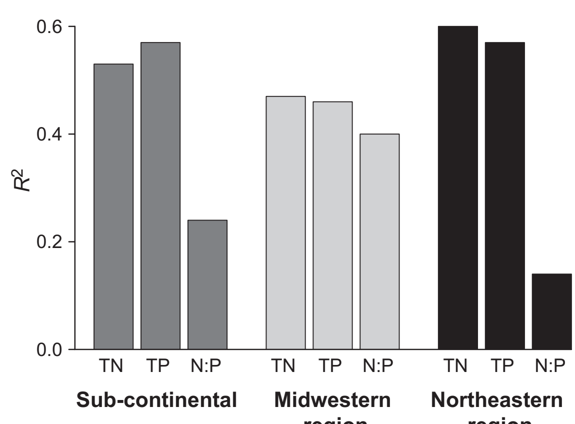

Fig. 3. R^2 for each response variable (TN, TP, N:P) for the sub-continental model, Northeastern region model, and Midwestern Region model.

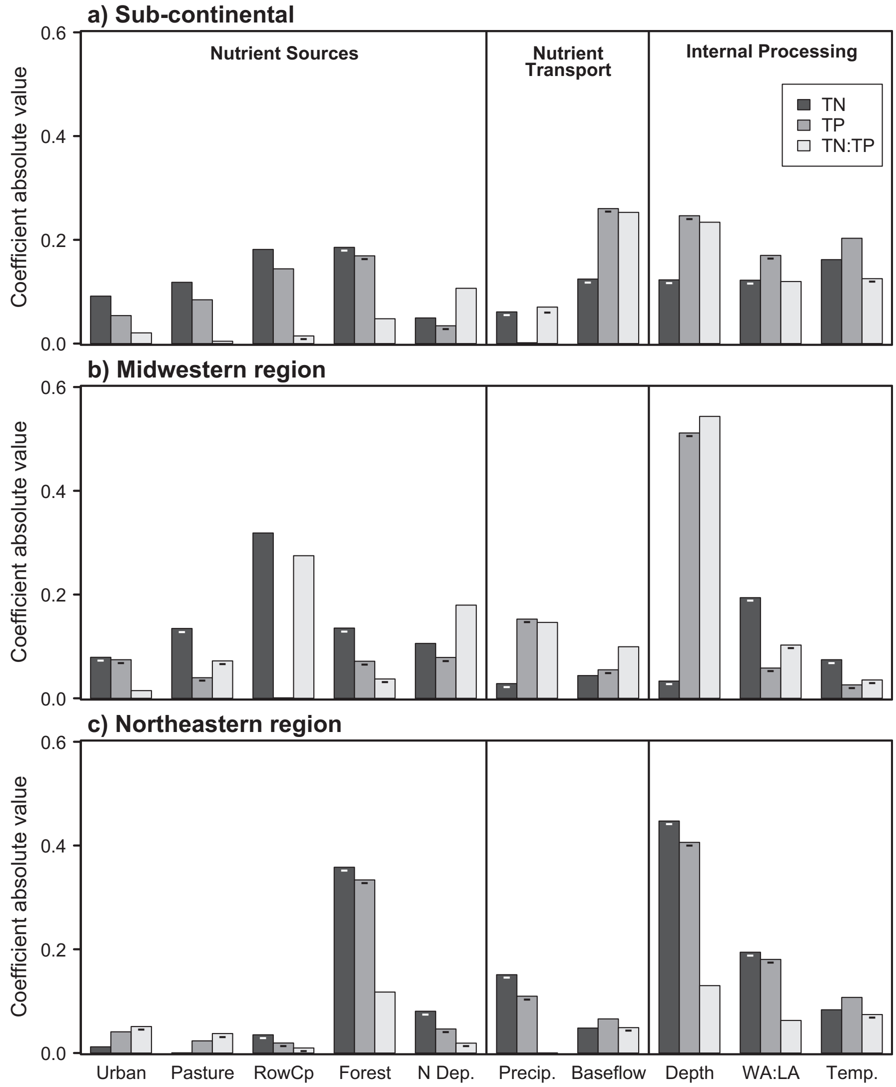

FIG. 4. Standardized regression coefficients for each response variable a) the Sub-continental extent, b) the Midwestern region, and c) the Northeastern region. The magnitude of each bar indicates the absolute value of the coefficient. Direction is indicated by signs on the bars; positive bars have no sign and negative coefficients have a minus sign.

VIP scores (above 0.8) for urban land use and residence time. Similarly, in the Midwestern region, two internal processing drivers (lake depth and residence time) and one nutrient source (row crop agriculture) variable were important, and forest land use was marginally important. In both regions, VIP scores and effect sizes for lake depth were largest, followed by the land use variable that was important in each region (Fig. 4, Table 2).

For N:P stoichiometry, effect sizes for most drivers were relatively low, especially in the sub-continental extent and the Northeastern regions, and the largest N:P effects were for drivers that had strong differences in coefficients for N and P concentrations. Hydrology (baseflow) and lake depth had the strongest effects on N:P at the sub-continental extent, corresponding to approximately two times stronger negative effects of both variables on P compared to N. All effect sizes in the Northeastern region model were comparable for N and P, leading to almost no effects of any driver on stoichiometry (Fig. 4c), and low R^2 for N:P stoichiometry (Fig. 3). In the Midwestern region, however, two drivers had different relationships with N and P and strong relationships with N:P stoichiometry: row crop agriculture had a strong positive effect on N but no effect on P, and depth had a strong negative effect on P but no effect on N (Fig. 4b).

DISCUSSION

Our results demonstrate that drivers related to nutrient loading and internal lake nutrient processing explained much less variation in N:P stoichiometry compared to individual concentrations of N and P. We

TABLE 2. Variable importance for projection (VIP) scores for models for each region.

Variable	Sub-Continental	Northeastern	Midwestern
Nutrient sources			
Pasture agriculture (%)	0.87	0.61	0.79
Row crop agriculture (%)	**1.3**	0.18	**1.56**
Urban land use (%)	0.66	0.82	0.64
Forest land use (%)	**1.4**	**1.67**	0.91
N deposition (kg/ha)	0.29	0.36	0.25
Nutrient transport			
Precipitation, 30-yr normal (mm)	0.40	0.09	0.66
Baseflow (%)	**1.1**	0.76	0.03
Internal processing			
Maximum depth (m)	**1.1**	**1.8**	**1.9**
Residence time (LA:WA)	**1.0**	0.90	**1.1**
Temperature, 30-yr normal (°C)	**1.3**	**1.2**	0.45

Note: Scores for important variables (VIP > 1.0) are shown in boldface type.

observed major differences across scales and ecological context, suggesting that relationships are context dependent and that the same drivers can affect both nutrients in a parallel way in some regions but only a single nutrient in others, and that both single and parallel response scenarios in Fig. 1 can occur. This contrasting pattern between drivers and responses of two individual nutrients can explain relationships between drivers and stoichiometry. Specifically, in the Northeastern region and, to a lesser extent, at the sub-continental scale, most drivers were related to N and P concentrations in similar ways. This, as expected, led to weak relationships between the same drivers and N:P stoichiometry (Fig. 1). In contrast, there was a single nutrient response for some drivers in the Midwestern region, leading to explanatory power for stoichiometry that was comparable to N and P concentrations (Fig. 1). The differences between the relatively undisturbed Northeastern region and relatively impacted Midwestern region suggest that human activity may decouple N and P, leading to single nutrient responses and better prediction of N:P stoichiometry in regions with high anthropogenic activity.

Previous work in the agricultural Midwest supports our results. Results from Iowa demonstrated that N:P stoichiometry could be explained by land use because N was associated with row crop agriculture while P was associated with pasture agriculture (Arbuckle and Downing 2001). Our results support the idea that there is a strong single nutrient association between N and row crop agriculture. However, we found that lake depth, rather than pasture, had a strong single nutrient relationship with P, suggesting that N is driven by nutrient inputs while internal processing drives P concentrations. Previous mass balance studies from reservoirs in the Midwestern United States support the conclusion that lake stoichiometry can reflect both nutrient sources and internal processing. Specifically, N:P of inputs to reservoirs varied with agricultural land use in the catchment, leading to different water column N:P but no differences in N:P of sediment burial, possibly because of denitrification (Vanni et al. 2011). Similarly, high denitrification rates in productive reservoirs lead to relatively low N:P of retained nutrients in eutrophic reservoirs compared to mesotrophic reservoirs (Grantz et al. 2014). On a broader spatial scale, Powers et al. (2014) suggested high denitrification and high P burial by lentic systems across the state of Wisconsin, especially in years with high nutrient loading.

Differences in the N and P cycles within lakes from studies in the Midwestern United States or other areas with agricultural or mixed land use might not be as pronounced in regions with uniformly low nutrient loading. This could explain our results from the Northeastern region, where we observed parallel nutrient responses for both nutrient loading and internal processing variables and could not explain variation in stoichiometry. Other recent broad-scale analyses supported the idea that anthropogenic activity might decouple N and P cycles, for example, P accumulates faster than N in lakes that are heavily impacted by humans (Yan et al. 2016).

While we identified agricultural land use as a regionally important nutrient source, nitrogen deposition might have similar effects and has been identified as a driver of single nutrient responses and stoichiometry in Scandinavia and the U.S. Rocky Mountains (Elser et al. 2009, Hessen et al. 2009, Bergström et al. 2013). N deposition did not have strong effects in our study areas. Previous work in an area similar to our Northeastern region found some associations between lake stoichiometry and N deposition (Crowley et al. 2012), but only within the Adirondacks (New York) and not in the broader Northeastern United States. Crowley et al. (2012) speculated that differences between the Northeastern United States and the Adirondacks sub-region were because deposition in parts of the Northeast might be insufficient to change in lake N, which is also likely true in our Northeastern analysis. The lack of a deposition signal may also be because our approach does not account for temporal variability; nitrogen deposition across our study region has changed over the last 20–30 yr. Ammonium deposition is increasing in the Midwestern region, while nitrate deposition is declining in the Northeastern region (Du et al. 2014), and N deposition rates have been associated with lake N trends (Oliver et al., *in revision*). Though current deposition inputs exceed that of the critical load for lakes in the Midwest and Northeast U.S. (Du et al. 2014), our results suggest that strong land use signals and the temporal variability in N deposition limit the relationship between lake stoichiometry and atmospheric deposition.

In addition to the effects of nutrient sources, strong relationships between lake depth and nutrients in nearly all analyses confirm that internal processing is a widespread and key control on nutrients and sometimes stoichiometry. The association between morphometry and P has been recognized for decades based on mechanistic P loading models (Vollenweider 1975); more recently, broad-scale studies have also identified lake depth as an important predictor of both N and P concentrations (Taranu and Gregory-Eaves 2008, Knoll et al. 2015, Read et al. 2015). There are many possible mechanisms that link lake depth and nutrient concentrations (e.g., lake volume to sediment ratio, particle settling times), and one possible is that depth and residence time covary and nutrient removal for both N and P increases with residence time (Vollenweider 1975, Harrison et al. 2009). However, the role of internal processing for predicting stoichiometry may only be important when nutrients inputs are relatively high or highly variable, possibly because extremely high N loading in agricultural watersheds can overwhelm any internal processing effects on N (Seitzinger et al. 2006) while high P loading, coupled with shallow depths, could lead to higher internal loads. Lake depth was often not included as a predictor of stoichiometry in previous studies (Hessen et al. 2009, Elser et al. 2010, Yan et al. 2016) likely because depth data are less widely available than other variables that can be remotely sensed or are measured consistently across space. Predictive models of depth have high uncertainty (Hollister et al. 2011, Heathcote et al. 2015, Oliver et al., *in revision*). However, our results show that including lake depth data in broad-scale predictions of lake nutrient stoichiometry is critical because the differential influence of depth on N vs. P across broad spatial extents is important for explaining variation in N:P.

The importance of broad-scale studies in understanding lake nutrient processes

Our approach shows how regional to continental-scale studies are useful for identifying spatial patterns of stoichiometric controls that depend on ecological context, and research at different spatial scales can provide complementary or unique insights. Whereas studies of individual or few lakes suggest differences among lakes and regions, spatial patterns are difficult to build from local studies. Our results and previous work (Cheruvelil et al. 2013) generally suggest that regional-level analyses of lakes with relatively homogenous ecological context are likely to differ from sub-continental, continental, or global analyses that include a wider range of ecological context gradients. We show that key controls on stoichiometry and nutrients vary across study regions with different ecological context, and that the single vs. parallel nutrient response can differ across regions (Fig. 1B). In particular, our results and another recent paper (Yan et al. 2016) demonstrate that N and P cycles are more likely to differ in areas with high human impact; hence, more mechanistic work on N and P cycling in regions with impacted vs. pristine watersheds may identify fundamental differences among regions. In addition, inferring mechanisms at the global scale might be even more difficult than the regional scale because previous global-scale studies have related stoichiometry to broad-scale, spatially structured predictors such as latitude (Abell et al. 2012) and climate (Chen et al. 2015) that might not be easy to differentiate from regional and local controls on nutrient cycles.

Additional sources of variation in lake nutrients

We were able to explain a relatively high proportion of variation in lake nutrient concentrations, and sometimes stoichiometry, using broad-scale drivers that are easily obtained from GIS maps. However, approximately 40–60% of the variation in sub-continental and regional study extents was left unexplained. We expect that much of this variation might be attributed to variables like lake biology. For example, the introduction of species can have profound influences on nutrient cycles, including increased nutrients that resulted from carp introductions in reservoirs (Dibble and Kovalenko 2009), and redistribution of nutrients from the introduction of zebra mussels to lakes (Hecky et al. 2004). Excretion of N and P by animals can also have strong effects on stoichiometry, with strong variation in N:P excretion within and across fish species (Torres and Vanni 2007, Wilson and Xenopoulos 2010), and terrestrial animals that cause nutrient inputs to freshwaters (Post et al. 1998, Subalusky et al. 2015, Dessborn et al. 2016). With increasing availability of broad-scale databases on biota, we may be able to incorporate such data into future studies of lake stoichiometry.

Further, the drivers included in our analysis cover a comprehensive range of nutrient sources, transport modes, and internal processing variables that are known to relate to lake nutrients, but they are still simplifications because they integrate across time and space. Improvements in measurements of these drivers may help explain further variation in nutrient concentrations and stoichiometry. For example, agricultural land use data might be improved by measuring agricultural practices such as tillage or fertilizer application rates, or the density of animals in a watershed, and urban land use data might be improved by including information about sewage treatment or population density. Such variables have been shown to be important for nutrient loading from land to water (Kronvang et al. 2005, 2008). Legacy of soil nutrients might also be important nutrient sources to freshwaters in agricultural regions, so more detailed information about terrestrial nutrient pools could lead to better prediction of lake nutrients (Jarvie et al. 2013, Van Meter and Basu 2015, Powers et al. 2016). Incorporating climate data associated with lake nutrient samples might also be important. In this study, we used 30-yr normal indices for temperature and precipitation as climate indicators, but the potential impacts of climate change on surface water quality are complex and remain unclear (Whitehead and Crossman 2012). More temporally specific climate indices and water temperature measurements could capture the effects of temperature and precipitation on stratification (Kraemer et al. 2015), biology (Magnuson et al. 1997, Mooij et al. 2005), and other factors that might influence internal nutrient cycles.

Conclusions

Lake nutrient stoichiometry had mostly weak relationships with known drivers of lake nutrient concentrations. We observed high context dependency in relating nutrient sources, transport and internal processing to lake nutrients and stoichiometry. Important drivers of nutrients and stoichiometry varied across regions and differed from previous studies in other parts of the world. In particular, controls on stoichiometry were different in an intensive agricultural region compared to a forested region, suggesting that anthropogenic impact leads to fundamental differences in our ability to predict stoichiometry. Stoichiometry can be highly variable in lakes relative to other systems (e.g., oceans), perhaps because of connections to the terrestrial landscape, and our results demonstrate that predicting stoichiometry is more challenging than predicting nutrient concentrations. However, being able to predict stoichiometry is especially important given its strong effects on a variety of ecological processes, including primary production (Conley et al. 2009, Paerl et al. 2016) and food webs (Elser et al. 2010).

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Data Availability

Data associated with this paper have been deposited in the Long Term Ecological Research Network Data Portal https://doi.org/10.6073/pasta/3abb4a56e76a52a12a366a338fc07dd8