

Anthropogenic land use is associated with N-fixing cyanobacterial dominance in lakes across the continental United States

Jonathan P. Doubek¹ · Cayelan C. Carey¹ · Bradley J. Cardinale²

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Abstract Cyanobacteria cause many water quality problems in lakes worldwide. Although many studies have examined factors that influence the structure of cyanobacterial communities, few have explicitly compared the effects of within-lake conditions (e.g., nutrient concentrations) and watershed parameters (e.g., land use) on a diverse array of cyanobacterial taxa. Here, we analyzed data from the 2007 U.S. Environmental Protection Agency's National Lakes Assessment to quantify how lakeshore anthropogenic land use, nutrient concentrations and ratios, and surface water temperatures predict cyanobacterial biovolume and dominance in 236 naturally-formed lakes spanning the continental U.S. We observed that anthropogenic lakeshore land use was the best predictor for cyanobacterial dominance, whereas in-lake nitrogen (N) and phosphorus (P) concentrations were the best predictors for cyanobacterial biovolume. Our analyses suggest that anthropogenic land use may influence cyanobacterial dominance via means other than increased nutrient concentrations. The sum of agricultural and human-developed lakeshore land use was the best predictor of N-fixing cyanobacterial dominance, but there was no significant relationship between anthropogenic land use and non-N-

fixing cyanobacterial dominance. In addition, we observed a total N:P ratio threshold for cyanobacterial dominance in the phytoplankton community (150:1) that was much higher than previously reported ratios. Consequently, management strategies to control cyanobacteria need to account for eco-physiological variation among different cyanobacterial taxa, and should consider nutrients *and* the other effects of land use to control overall lake cyanobacterial biovolume and cyanobacterial dominance, as the two cyanobacterial metrics may be sensitive to different drivers.

Keywords Cyanobacterial bloom · Eutrophication · Freshwater lakes · Management · Phytoplankton

Introduction

While cyanobacteria are commonly found in many lake phytoplankton communities (e.g., Smith 1983; Downing et al. 2001; Ptacnik et al. 2008), certain cyanobacterial taxa can become a nuisance when they reach high densities and form blooms (e.g., Bartram and Chorus 1999; Wilson and Carpenter 1999; Codd et al. 2005; Dodds et al. 2009). Although many studies aggregate cyanobacteria into one bulk group to study the drivers of bloom formation, cyanobacteria represent an extremely heterogeneous array of taxa (e.g., Bartram and Chorus 1999; Dokulil and Teubner 2000; Huisman et al. 2005; Carey et al. 2012a; Rigosi et al. 2014). For example, not all cyanobacterial taxa form blooms, and some taxa are more likely to create surface scums while others dominate the metalimnion (Ibelings et al. 1991; Bormans et al. 1999; Brookes et al. 1999, 2002). In addition, some genera are able to fix nitrogen (N) from the atmosphere or from other sources

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✉ Jonathan P. Doubek
jpdoubek@vt.edu

¹ Department of Biological Sciences, Virginia Tech, 1405 Perry Street, Blacksburg, VA 24061-0406, USA

² School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, MI 48109-1041, USA

(Bergman et al. 1997; Bartram and Chorus 1999), allowing these taxa to become dominant when N is limiting, or when there is much greater phosphorus (P) relative to N (Smith 1983). Because cyanobacteria represent a diverse and heterogeneous group, it is important to examine the drivers of biovolume and dominance for individual cyanobacterial taxa, in addition to total cyanobacteria, because they are likely sensitive to different factors (Rigosi et al. 2014).

It has long been known that humans can indirectly influence phytoplankton communities in individual lakes by converting the surrounding terrestrial ecosystems into agricultural or urban habitats (e.g., Carpenter et al. 1998; Hall et al. 1999; Schindler 2006). These forms of altered land use are often associated with an increase in applied fertilizers and agricultural runoff (Sharpley et al. 1994, 2001; Vanni et al. 2011; Schindler et al. 2012). In addition, increased impervious surfaces and runoff from the built environment increase N and P inputs into lakes that can stimulate cyanobacteria (Hall et al. 1999; Jeppesen et al. 2005; Schindler 2006).

However, land use may have other impacts on cyanobacterial communities in addition to increasing N and P concentrations (Soranno et al. 1996; Carpenter et al. 2011; Nielsen et al. 2012). For example, the conversion of forest into agricultural or urban land in a watershed may increase lake water temperature because of the increased flow and temperature of water draining impervious surfaces (LeBlanc et al. 1997; Fraterrigo and Downing 2008; Thompson et al. 2008a, b), and because of warmer air-water temperature exchange, which is due to the increased air temperatures associated with lakeshore land use development (Otieno and Anyah 2012; Hu et al. 2015). Increased water temperature may subsequently stimulate cyanobacteria because they have higher optimum temperatures for growth than other phytoplankton taxa (reviewed in Reynolds 2006; but see Lüring et al. 2013), promoting their dominance in the phytoplankton community as water temperatures increase above 20 °C (Paerl and Otten 2013). Consequently, because of these additional aspects of land use, it is important to examine the other effects of lakeshore land use on cyanobacteria in addition to the effects of within-lake nutrient concentrations.

To the best of our knowledge, only a few studies have directly examined the effects of quantitative land use metrics on phytoplankton communities, and those studies have primarily focused on individual lakes or regions (Hall et al. 1999; Knoll et al. 2003; Vanni et al. 2011; Beaver et al. 2012; Katsiapi et al. 2012; Paul et al. 2012). Therefore, surprisingly little is known about the relationship between cyanobacteria and lakeshore land use because most studies on cyanobacteria have focused solely on the effects of within-lake nutrient concentrations (e.g.,

Downing et al. 2001; Jeppesen et al. 2005; Schindler et al. 2008; Conley et al. 2009; Paerl 2009; Xu et al. 2010).

It is well-known that patterns between land use and in-lake nutrient concentrations differ widely across different ecoregions in the U.S. because of their varying climate, geology, land use history, and other factors (Fraterrigo and Downing 2008; Beaver et al. 2012). These differences among ecoregions can result in baseline differences in lake water quality (e.g., Dodds et al. 2009; Fergus et al. 2011; Wagner et al. 2011). We are, however, just beginning to amass the data needed to assess the large-scale, long-term generality of such patterns to determine how humans influence cyanobacterial dominance at the continental scale.

Here, we used the 2007 U.S. Environmental Protection Agency's (EPA) National Lakes Assessment (NLA) dataset to examine how lakeshore land use (i.e., the proportion of different land use categories around a lake's perimeter), in addition to nutrient concentrations and surface water temperatures (Beaulieu et al. 2013; Rigosi et al. 2014), are associated with total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance across 236 lakes spanning the continental U.S. Although not all lakes or all states in the U.S. were included, this study represents the broadest geographical analysis of which we are aware that examines the relationships between land use and phytoplankton. Since Beaulieu et al. (2013) found that phytoplankton in human-made reservoirs responded differently than phytoplankton in naturally-formed lakes to nutrients and temperature using this NLA dataset, we focused our analyses on natural lakes. Using this dataset, we asked the following questions: (1) At the U.S. and ecoregion scales, what is the relationship between anthropogenic lakeshore land use and total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance?; (2) How variable are the responses of N-fixing, non-N-fixing, and individual cyanobacterial taxa to anthropogenic land use, in-lake nutrient concentrations and ratios, and surface water temperature?; and (3) Do phytoplankton and cyanobacterial communities respond differently to land use vs. in-lake nutrient concentrations; i.e., are there other ways by which land use can affect phytoplankton in addition to increased nutrient concentrations?

Methods

NLA dataset

To answer our questions, we analyzed data collected as part of the U.S. EPA's NLA. The NLA represents a collaboration among EPA research scientists and state agencies, tribes, academic and other federal agencies to collect

baseline measurements of the physical, chemical, and biotic conditions of U.S. lakes. To be included in the NLA, naturally-formed or human-made lakes had to be located in the continental U.S., have greater than 4 ha in surface area, and a minimum depth of 1 m. As noted above, we restricted our analyses to the naturally-formed lakes in the NLA (Beaulieu et al. 2013).

Every lake in the NLA survey was sampled during May through October in 2007. Field crews followed standardized protocols to survey the physical (e.g., surface water temperature), chemical [e.g., concentrations of total N and P (TN and TP)], and biological conditions (phytoplankton abundances and biovolume) of each lake. Surface water temperatures were recorded via a multi-parameter water quality sonde that measured temperatures at 0.5–1 m increments from the surface to just above the lake sediments. All data, metadata, and sampling and laboratory methods from the NLA survey are publicly available at http://water.epa.gov/type/lakes/lakessurvey_index.cfm.

Biological data

Phytoplankton were collected from the deepest site in each lake by an integrated tube sampler that extended from the water's surface to 2 m depth. This volume was homogenized and preserved in the field with Lugol's solution before being subsampled by trained taxonomists, who identified phytoplankton for each lake to at least the genus level using Utermöhl or Palmer-Maloney counting chambers. At least 300 individual phytoplankton cells were identified and enumerated within a random, systematic field of view. Phytoplankton samples were processed across several different laboratories, and ten percent of each lab's samples were reanalyzed for quality control. In addition, there was external quality control of the phytoplankton analyses by independent taxonomists, who audited ten percent of each laboratory's samples. Additional information about phytoplankton field and lab protocols is available at: http://www.epa.gov/owow/LAKES/lakessurvey/pdf/qualityassuranceplan_draft.pdf.

Cell densities (cells/mL) were multiplied by the cell biovolumes of each genus ($\mu\text{m}^3/\text{cell}$) to estimate the total biovolume of each phytoplankton genus per lake. For some entries in the NLA dataset, species biovolumes were not measured, especially for rare taxa. Because a substantial number of phytoplankton biovolume calculations were missing from many lakes, we decided *a priori* to exclude lakes from subsequent analyses if (1) greater than 30 percent of the taxa identified in the lake lacked estimates of cell biovolumes, or (2) the lake had fewer than three species with biovolume data. These cut-offs were arbitrary, but they were made *a priori* and applied consistently to ensure that the final set of lakes included in the dataset had

robust and nearly complete estimates of plankton biovolume. We explored a range of biovolume thresholds and found the same qualitative conclusions as presented in the remainder of this paper.

In total, 236 naturally-formed lakes met our criteria for being included in the analyses. Most lakes in the NLA dataset were sampled once, but in the few instances where replicate samples were taken, we averaged phytoplankton biovolumes across the replicates that met our criteria. Our analyses did not include dinoflagellates because only one dinoflagellate genus had biovolume data. We also excluded a diatom group called "Diatoms (dead)", which represented empty silicate frustules in the water column, and a group called "Unknown Algae".

Land use

Land use within a 200 m wide perimeter around each of the 236 lakes (hereafter termed lakeshore land use) was quantified by the United States Geological Survey's (USGS) National Land Cover Dataset (NLCD), which was condensed and reported by the NLA. The NLA only reported lakeshore land use within the 200 m perimeter of each lake. The land use categories in the dataset were 'developed' (i.e., amount of impervious surface cover), 'barren', 'forested', 'shrubland', 'grass', 'pasture', 'crop', and 'wetland'. Total agriculture represented the sum of pasture and crop land use types. A full list and description of the different NLCD land use cover types can be found at <http://www.mrlc.gov>.

The primary land use metric that we used in our analyses was the proportion of each terrestrial land use category around each lake's perimeter. We used proportion (not total area) of each lakeshore land use category to account for the size of each lake (because larger lakes have larger total buffer areas), and so lakes of different sizes could be accurately compared. Since prior studies have observed that human-dominated lakeshore land use was positively associated with cyanobacteria (Hall et al. 1999; Katsiapi et al. 2012; Paul et al. 2012), we focused our analyses on the agriculture and developed land use categories. We examined the proportions of lakeshore land use dominated by pasture, crop, total agriculture (i.e., pasture and crop summed), human developed, and the sum of total agriculture and developed land (hereafter, AD land use). We examined all of these lakeshore land use categories independently to quantify which anthropogenic land use category was the best predictor for total phytoplankton, cyanobacterial biovolume, and cyanobacterial dominance.

Lake nutrient concentrations

The NLA collected lake water for TN and TP laboratory analyses with an integrated water sampler that extended

from the water's surface to 2 m depth. All water chemistry samples were analyzed in laboratories using standard operating protocols administered by the U.S. EPA's Western Ecology Division. These data were used to assess if there were relationships between nutrient concentrations and AD land use, and between nutrient concentrations and total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance across the U.S.

Statistical analyses

We used a regression modeling framework for examining the effects of land use, nutrient concentrations, and other factors on phytoplankton communities in lakes across the U.S. We constructed least-squares linear regressions to analyze the separate effects of all anthropogenic land use categories (pasture, crop, total agriculture, developed, and AD land use) and nutrients (TN and TP) on total phytoplankton biovolume, total cyanobacterial biovolume, and cyanobacterial dominance across the U.S. We also converted TN and TP to their molar ratios to examine how TN:TP was associated with lake cyanobacterial dominance (following Smith 1983; Downing et al. 2001). We determined the anthropogenic land use category that was the strongest predictor for aggregated cyanobacterial dominance at the U.S. scale by the lowest corrected AIC (AICc) value, which was the focal land use variable (AD land use) used in subsequent analyses to examine the effects of anthropogenic land use at the ecoregion scale and on individual cyanobacterial genera. All analyses were performed in JMP v. 11.0. (SAS Institute, Cary, NC, USA).

We examined whether U.S. scale patterns of land use on phytoplankton communities were consistent within select U.S. ecoregions. We divided up lakes into their respective EPA level III ecoregions, which the EPA delineates as fourteen areas in the U.S. that are characterized by similar hydrology, vegetation, climate, and soil (Fig. 1). This allowed us to assess whether the trends observed at the U.S. scale were driven by lakes in a particular ecoregion, and if land use-cyanobacterial relationships were similar in different ecoregions. For these additional analyses, we limited our analyses to ecoregions that had >10 natural lakes that also met the phytoplankton biovolume criteria described above. Total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance were analyzed by our focal anthropogenic land use variable (AD land use) nested within ecoregion to account for regional differences. Together, these ecoregions covered a significant extent and diversity of regions in the U.S.

In addition to overall cyanobacterial biovolume and dominance, we compared the effects of anthropogenic land use on several different cyanobacterial groups:

N-fixing cyanobacteria, non-N-fixing cyanobacteria, and all of the observed, individual cyanobacterial genera (14 genera in total; Bergman et al. 1997; Bartram and Chorus 1999).

We explored how surface water temperature, another variable potentially associated with land use, affected total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance with least-squares linear regressions. We also included linear relationships between lake depth and surface area vs. surface water temperature as these variables may be associated with one another (e.g., Gorham 1964; Gorham and Boyce 1989), and confound potential significant relationships between AD land use and surface water temperature. However, climatic variables were not included in these analyses, which could potentially confound associations between AD land use and surface water temperature.

To meet assumptions of normality, total lake phytoplankton biovolume, cyanobacterial biovolume, TN, TP, TN:TP, lake depth, and lake surface area were ln-transformed. Because many of the independent variables were correlated (e.g., TN vs. TP: $r = 0.89$, $P < 0.0001$; agriculture vs. developed land use: $r = 0.34$, $P < 0.0001$; AD vs. other individual land use categories: $r \geq 0.54$, $P < 0.0001$, Pearson product-moment correlations; see Table S1 in the supplementary material for all included variable comparisons), they were not included in the same regression models, and we consequently estimated and compared many univariate linear regression models to answer our research questions. While there are more complex statistical approaches that can be used to examine the effects of land use and nutrients on phytoplankton, our initial analyses were focused on exploring and establishing the direction and relative strength of these individual relationships. Variables expressed as proportions (all anthropogenic land use types and proportional biovolumes of cyanobacteria) were logit-transformed prior to analyses (Warton and Hui 2011). If the proportions had zero values, we added the minimum positive observation to each value prior to logit-transformation so those data could be included in the analyses (following Warton and Hui 2011). The addition of the X_{\min} value changed parameter estimates but did not alter the significance or relative importance of the predictors in the regression models. However, the individual cyanobacterial genera often had many zero values, and so these zero values were excluded to obviate many low values having an extreme influence on the land use and individual cyanobacterial genera comparisons. A list of all included predictor and response variables in the analyses, as well as their means, standard deviations, maximum and minimum values are recorded in Table 1.

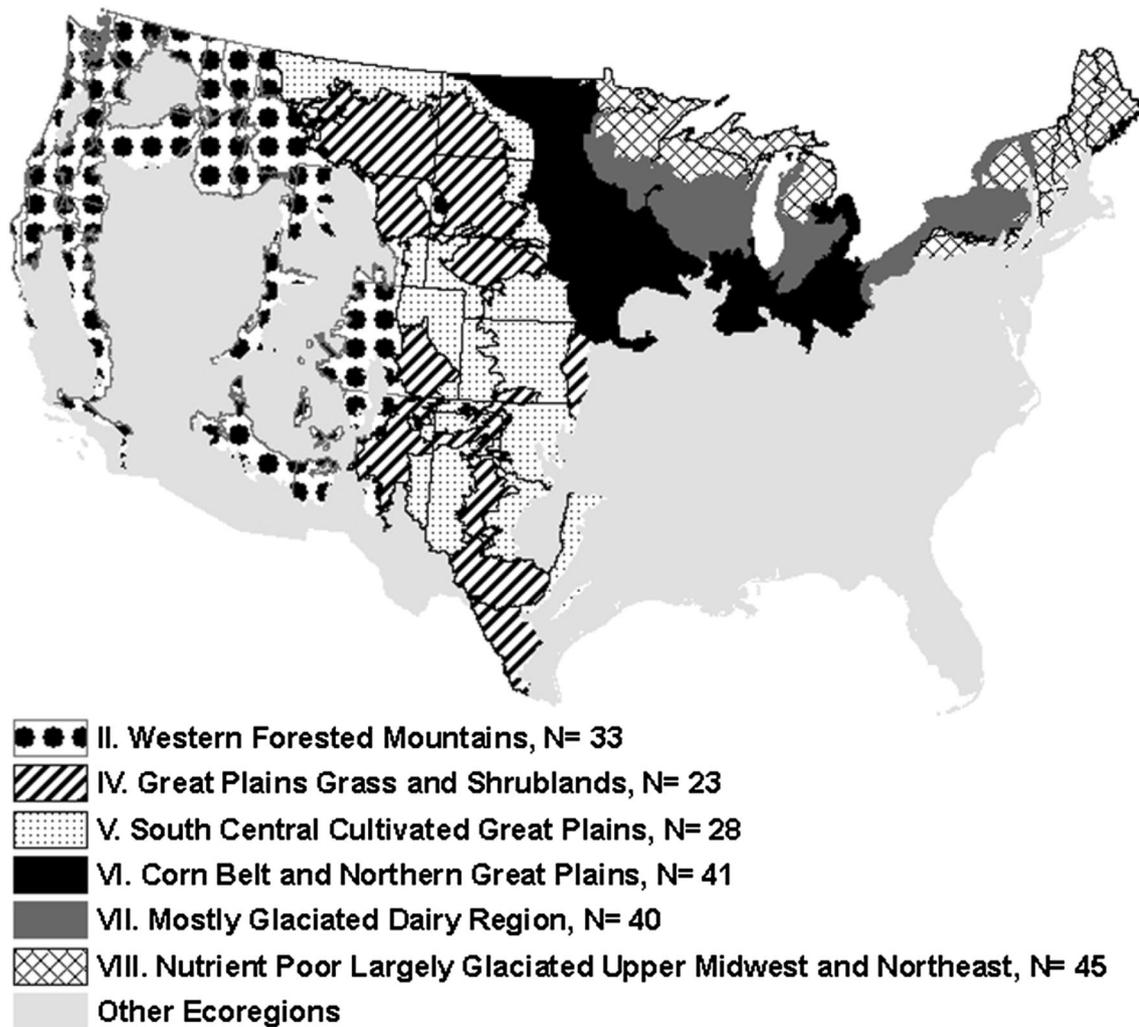


Fig. 1 A map of the EPA level III ecoregions across the U.S included in the ecoregion analyses. Only EPA level III ecoregions with at least 10 naturally-formed lakes were included for these comparisons. The

six focal ecoregions together covered a large extent and diversity of regions of the U.S. *N* refers to the natural lake sample size within each ecoregion

Results

Question 1: anthropogenic land use vs. total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance at the U.S. and ecoregion scales

As expected, we observed significant positive relationships individually between crop, pasture, agriculture, and AD land use, and total phytoplankton biovolume in lakes across the U.S. (all $P \leq 0.02$; Fig. 2; all regression equations and statistics given in Table 2). However, there was only a marginally significant, positive relationship between developed land use and total phytoplankton biovolume ($P = 0.09$), thus, most of a lake's total phytoplankton biovolume in the AD land use category was explained by the agricultural components. Consequently, of the five

anthropogenic land use categories, agriculture and AD land use equally explained the most variation in total phytoplankton biovolume (both $R^2 = 0.05$).

Of the anthropogenic land use categories, AD land use was the best predictor of total cyanobacterial biovolume and contributed three times more variation in total cyanobacterial biovolume than the biovolume of the aggregated total phytoplankton community (Table 2). All anthropogenic land use types were individually positively and significantly related to higher total cyanobacterial biovolume (all $P \leq 0.0002$; Fig. 2; Table 2). Agricultural land use ($R^2 = 0.12$) explained two times more variation in total cyanobacterial biovolume than did developed land use ($R^2 = 0.06$).

Similarly, all anthropogenic land use types were significantly and positively associated with cyanobacterial dominance ($P \leq 0.002$ in all cases; Fig. 2; Table 2). AD

Table 1 A list of all the variables included in the analyses, as well as their units, means, standard deviations, and minimum and maximum values

Variable	Units	Mean	SD	Min	Max
Lakeshore land use type					
Pasture	%	4.3	11.8	0	90
Crop	%	10.4	18.9	0	80.5
Agriculture	%	14.7	22.8	0	100
Developed	%	13.1	18.9	0	100
Agriculture + developed	%	27.7	29.2	0	100
Physical variables					
Surface water temperature	°C	22.9	4.1	11.2	32
Lake depth	meters	9.4	11.3	0.6	50
Lake surface area	km ²	11.6	111	0.05	1670
Water chemistry					
TN	µg/L	2440	4130	28	26,100
TP	µg/L	200	370	1	2150
TN:TP	None	87.3	130	3.4	1420
Phytoplankton metrics					
Total phytoplankton biovolume	µm ³ /mL	7.3 × 10 ⁶	1.3 × 10 ⁷	2.9 × 10 ³	7.4 × 10 ⁷
Total cyanobacterial biovolume	µm ³ /mL	2.5 × 10 ⁶	6.3 × 10 ⁶	0	6.0 × 10 ⁷
Cyanobacterial dominance	%	30.9	31.0	0	98
N-fixing cyanobacterial dominance	%	19.0	28.0	0	98
Non-N-fixing cyanobacterial dominance	%	11.0	18.4	0	98

Detection limits for TN and TP were 20 and 4 µg/L, respectively, and some values of TP were below the detection limit

land use explained the most variation in cyanobacterial dominance out of the land use types ($R^2 = 0.15$), whereas pasture explained the least ($R^2 = 0.04$). Total agriculture individually explained more variation ($R^2 = 0.12$) in cyanobacterial dominance than total developed land ($R^2 = 0.08$). Cyanobacterial biovolume and dominance were strongly, but not perfectly, correlated ($r = 0.73$, $P < 0.0001$; Pearson product-moment correlation).

However, unlike the U.S. scale results, we did not observe a significant effect of land use nested within ecoregion on total phytoplankton biovolume ($P = 0.27$; Table 3). Not surprisingly, there was an ecoregion effect on total phytoplankton biovolume ($P < 0.0001$; Table 3), with the Western Forested Mountains (ecoregion II) having the lowest total phytoplankton biovolume and the Great Plains Grass and Shrublands (ecoregion IV) having the greatest phytoplankton biovolume.

AD land use nested within ecoregion was significantly associated with cyanobacterial biovolume and cyanobacterial dominance ($P \leq 0.009$ in both cases; Table 3). Certain ecoregions such as the Western Forested Mountains (ecoregion II) and the Nutrient Poor Largely Glaciated Upper Midwest and Northeast (ecoregion VIII) exhibited particularly strong, positive relationships between AD land use and cyanobacterial biovolume, and AD land use and cyanobacterial dominance ($P \leq 0.03$ in both cases;

Table 3), which drove the U.S. scale relationships. The other four ecoregions in the analysis generally had positive, but non-significant, relationships between land use and cyanobacterial biovolume and dominance (all $P > 0.05$). There were no significant differences among ecoregions in cyanobacterial dominance ($P = 0.23$; Fig. 3). However, there was a significant ecoregion effect of total cyanobacterial biovolume across ecoregions ($P = 0.007$), with ecoregions II and VIII having lower cyanobacterial biovolumes than two Corn Belt ecoregions (IV and VI; $P < 0.05$; Fig. 3).

Question 2: effects of land use, nutrient concentrations and ratios, and surface water temperatures on the dominance of N-fixing, non-N-fixing, and individual cyanobacterial genera

Overall, anthropogenic land use explained more variation in the dominance of N-fixing cyanobacteria than for the dominance of aggregated total cyanobacteria in the phytoplankton community. All anthropogenic land use categories were significantly and positively associated with N-fixing cyanobacterial dominance ($P < 0.0001$ in all cases; Table 2), with AD land use contributing more variation in N-fixing cyanobacterial dominance than any other land use category ($R^2 = 0.21$; Fig. 2). TN, TP, and

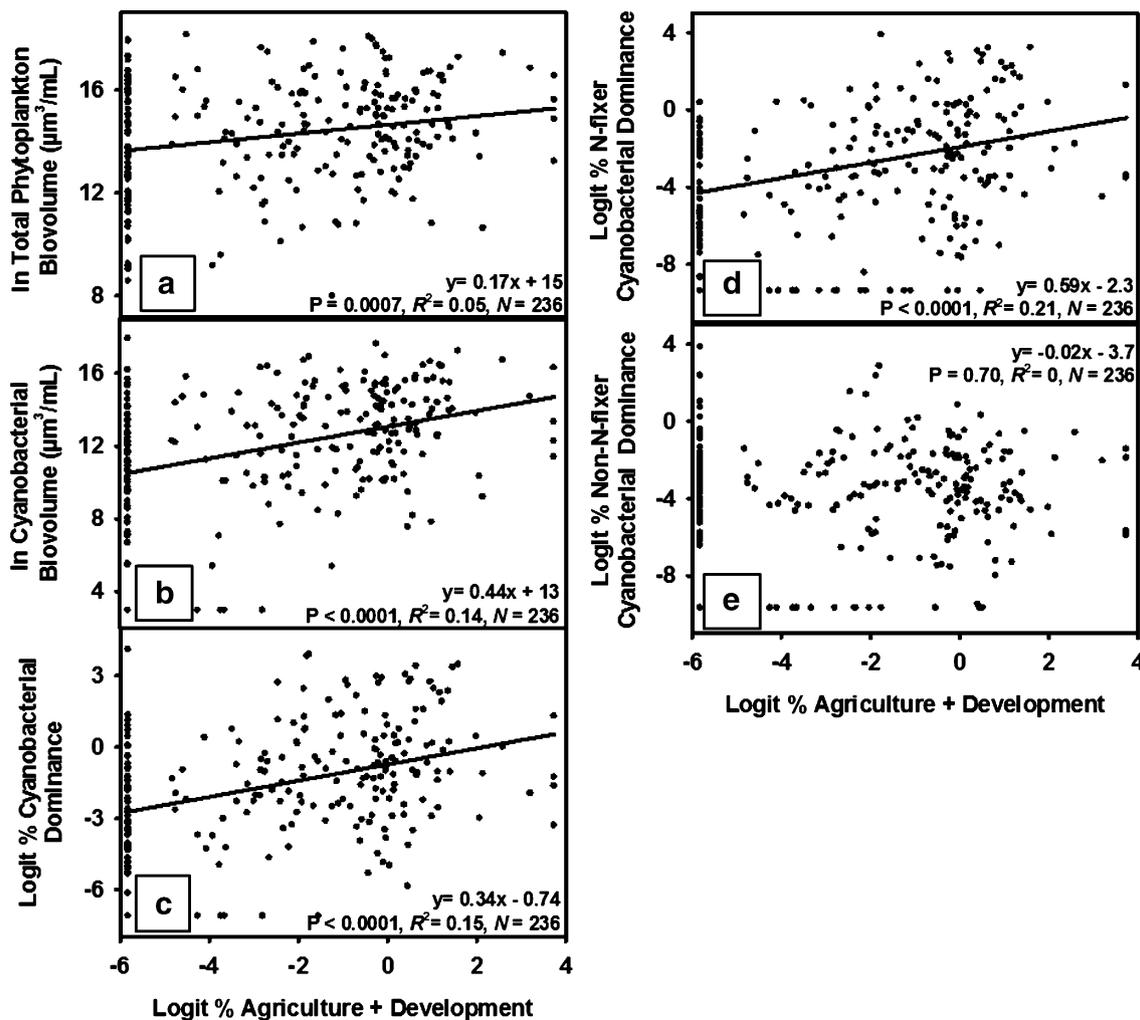


Fig. 2 The effects of logit-transformed % agriculture and developed land use in a 200 m perimeter around a lake on **a** total phytoplankton biovolume, **b** cyanobacterial biovolume, **c** cyanobacterial dominance,

d N-fixing cyanobacterial dominance, and **e** non-N-fixing cyanobacterial dominance

surface temperature were also each positively and significantly associated with N-fixing cyanobacterial dominance (all $P \leq 0.002$; Table 2). Surface temperature explained more U.S. variation ($R^2 = 0.07$) in N-fixing cyanobacterial dominance compared to lake nutrient concentrations ($R^2 = 0.02$ – 0.04).

Interestingly, while all anthropogenic land use categories were significantly associated with N-fixing cyanobacterial genera, there was no observed relationship between any land use category and the dominance of non-N-fixing cyanobacterial taxa ($P > 0.46$; Fig. 2; Table 2). As expected, TN was significantly and positively associated with non-N-fixing cyanobacterial dominance ($P = 0.01$), but there was no relationship between TP and non-N-fixing cyanobacterial dominance ($P = 0.36$). Surface temperature was also positively and significantly associated with non-N-fixing cyanobacterial dominance

($P = 0.03$), but surface temperature explained less ($R^2 = 0.02$) of the U.S. scale variation in non-N-fixing cyanobacteria compared to N-fixing cyanobacteria ($R^2 = 0.07$).

In general, AD land use had positive and significant effects on the dominance of individual N-fixing cyanobacterial genera, but there were no significant effects of any land use category predictor on non-N-fixing cyanobacterial genera (Fig. 4). The two most common N-fixing cyanobacterial genera in the NLA dataset, *Anabaena* and *Aphanizomenon*, both had positive and significant relationships with land use (both $P \leq 0.002$; Fig. 4). AD land use explained more variation in aggregated N-fixing cyanobacterial dominance ($R^2 = 0.21$) than in any individual genus: e.g., AD land use explained less of the U.S. scale variation in *Anabaena* dominance ($R^2 = 0.07$) and in *Aphanizomenon* dominance

Table 2 Summary statistics of the linear relationships between anthropogenic lakeshore land use types, nutrient concentrations, and surface water temperature on total phytoplankton biovolume, total cyanobacterial biovolume, cyanobacterial dominance, N-fixing cyanobacterial dominance, and non-N-fixing cyanobacterial dominance across 236 natural lakes in the U.S

Linear model	P value	R ²	AICc
Total phytoplankton biovolume (TPB)			
$\ln \text{TPB} = 7.90 + 0.93 \ln \text{TN}$	<0.0001	0.38	916
$\ln \text{TPB} = 11.9 + 0.65 \ln \text{TP}$	<0.0001	0.37	920
$\ln \text{TPB} = 14.9 + 0.16 \text{ logit agriculture}$	0.0005	0.05	1016
$\ln \text{TPB} = 14.6 + 0.17 \text{ logit agriculture} + \text{ developed}$	0.0007	0.05	1016
$\ln \text{TPB} = 14.9 + 0.13 \text{ logit crop}$	0.01	0.03	1022
$\ln \text{TPB} = 15.0 + 0.12 \text{ logit pasture}$	0.02	0.02	1022
$\ln \text{TPB} = 14.6 + 0.09 \text{ logit developed}$	0.09	0.01	1025
$\ln \text{TPB} = 13.4 + 0.04 \text{ surface temperature}$	0.27	0.01	1027
Total cyanobacterial biovolume (TCB)			
$\ln \text{TCB} = 3.45 + 1.26 \ln \text{TN}$	<0.0001	0.31	1131
$\ln \text{TCB} = 8.98 + 0.85 \ln \text{TP}$	<0.0001	0.28	1141
$\ln \text{TCB} = 13.1 + 0.44 \text{ logit agriculture} + \text{ developed}$	<0.0001	0.14	1183
$\ln \text{TCB} = 13.6 + 0.36 \text{ logit agriculture}$	<0.0001	0.12	1189
$\ln \text{TCB} = 13.6 + 0.33 \text{ logit crop}$	<0.0001	0.08	1199
$\ln \text{TCB} = 13.2 + 0.30 \text{ developed}$	<0.0001	0.06	1204
$\ln \text{TCB} = 7.68 + 0.19 \text{ surface temperature}$	<0.0001	0.06	1204
$\ln \text{TCB} = 13.8 + 0.29 \text{ logit pasture}$	0.0002	0.06	1205
Cyanobacterial dominance			
$\text{Logit cyanobacteria} = -0.74 + 0.34 \text{ logit agriculture} + \text{ developed}$	<0.0001	0.15	1059
$\text{Logit cyanobacteria} = -0.35 + 0.28 \text{ logit agriculture}$	<0.0001	0.12	1066
$\text{Logit cyanobacteria} = -0.08 + 0.30 \text{ logit crop}$	<0.0001	0.12	1067
$\text{Logit cyanobacteria} = -0.56 + 0.26 \text{ logit developed}$	<0.0001	0.08	1077
$\text{Logit cyanobacteria} = -5.24 + 0.16 \text{ surface temperature}$	<0.0001	0.08	1077
$\text{Logit cyanobacteria} = -4.48 + 0.44 \ln \text{TN}$	0.0001	0.06	1081
$\text{Logit cyanobacteria} = -2.58 + 0.30 \ln \text{TP}$	0.0002	0.06	1082
$\text{Logit cyanobacteria} = -0.39 + 0.19 \text{ logit pasture}$	0.002	0.04	1086
N-fixer dominance			
$\text{Logit N-fixer} = -2.34 + 0.59 \text{ logit agriculture} + \text{ developed}$	<0.0001	0.21	1216
$\text{Logit N-fixer} = -1.74 + 0.47 \text{ logit agriculture}$	<0.0001	0.16	1231
$\text{Logit N-fixer} = -1.49 + 0.46 \text{ logit crop}$	<0.0001	0.13	1239
$\text{Logit N-fixer} = -1.94 + 0.48 \text{ logit developed}$	<0.0001	0.12	1241
$\text{Logit N-fixer} = -1.46 + 0.37 \text{ logit pasture}$	<0.0001	0.08	1253
$\text{Logit N-fixer} = -8.85 + 0.23 \text{ surface temperature}$	<0.0001	0.07	1255
$\text{Logit N-fixer} = -5.03 + 0.38 \ln \text{TP}$	0.001	0.04	1261
$\text{Logit N-fixer} = -7.08 + 0.50 \ln \text{TN}$	0.002	0.04	1262
Non-N-fixer dominance			
$\text{Logit non-N-fixer} = -5.70 + 0.30 \ln \text{TN}$	0.01	0.03	1125
$\text{Logit non-N-fixer} = -5.63 + 0.09 \text{ surface temperature}$	0.03	0.02	1126
$\text{Logit non-N-fixer} = -3.90 + 0.08 \ln \text{TP}$	0.36	0.004	1130
$\text{Logit non-N-fixer} = -3.77 - 0.05 \text{ logit developed}$	0.47	0.002	1130
$\text{Logit non-N-fixer} = -3.71 - 0.03 \text{ logit agriculture}$	0.65	0.001	1131
$\text{Logit non-N-fixer} = -3.66 - 0.02 \text{ logit agriculture} + \text{ developed}$	0.70	0.001	1131
$\text{Logit non-N-fixer} = -3.68 - 0.02 \text{ logit crop}$	0.80	0.0003	1131
$\text{Logit non-N-fixer} = -3.64 - 0.01 \text{ logit pasture}$	0.92	0.00005	1131

Within each response variable, the regression models are listed in descending order of the best fit model, according to the lowest corrected AIC (AICc) value

TN total nitrogen, TP total phosphorus concentrations

Table 3 Variation in total phytoplankton, total cyanobacterial biovolume, and cyanobacterial dominance as a function of percent logit agriculture + developed lakeshore land use across six ecoregions in the U.S

Ecoregion	Total phytoplankton biovolume ($R^2 = 0.39$)	Cyanobacterial biovolume ($R^2 = 0.36$)	Cyanobacterial dominance ($R^2 = 0.22$)
II, $N = 33$	$\beta = 0.27$	$\beta = 0.78, P = 0.001$	$\beta = 0.56, P = 0.005$
IV, $N = 23$	$\beta = 0.34$	$\beta = 0.56$	$\beta = 0.18$
V, $N = 28$	$\beta = 0.01$	$\beta = 0.28$	$\beta = 0.24$
VI, $N = 41$	$\beta = 0.08$	$\beta = 0.24$	$\beta = 0.27$
VII, $N = 40$	$\beta = 0.19$	$\beta = 0.04$	$\beta = -0.37$
VIII, $N = 45$	$\beta = 0.22$	$\beta = 0.45, P = 0.02$	$\beta = 0.34, P = 0.03$

N refers to the sample size of natural lakes within each ecoregion, β refers to the magnitude of the slope in land use as a predictor for each respective dependent variable, and P-values were given in bold if results were significant ($P < 0.05$)

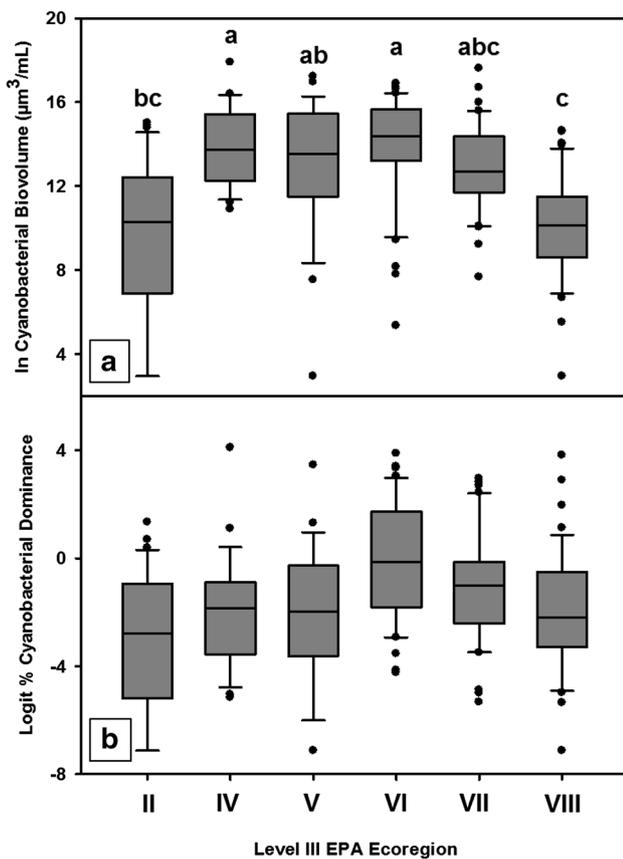


Fig. 3 Boxplots detailing the variation in **a** cyanobacterial biovolume, and **b** cyanobacterial dominance across our six focal ecoregions in the U.S. Letters above each boxplot denote statistical differences of cyanobacterial biovolume among ecoregions. There was no ecoregion effect of cyanobacterial dominance

($R^2 = 0.19$) compared to all N-fixers. AD land use was also positively associated with *Oscillatoria* ($P = 0.02, R^2 = 0.16$) and *Lyngbya* dominance ($P = 0.02, R^2 = 0.13$). There was no significant relationship between land use and the dominance of any non-N-fixing

cyanobacterial taxon, such as *Aphanocapsa* ($P = 0.13$) or *Microcystis* ($P = 0.57$; Fig. 4).

We also examined if there was a U.S. scale TN:TP ratio that predicted cyanobacterial dominance (Fig. 5). There was a significant negative relationship between the TN:TP ratio and total cyanobacterial dominance ($P = 0.047, R^2 = 0.02$; cyanobacterial dominance = $-0.33 \times \text{TN:TP ratio} - 0.18$; Fig. 5). Cyanobacteria were regularly able to dominate (i.e., exhibit $\geq 50\%$ of total biovolume in the phytoplankton community) in lakes with TN:TP up to $\sim 150:1$, regardless of whether or not the dominant cyanobacterial taxon was N-fixing or non-N-fixing. However, in lakes with TN:TP $> 150:1$, the cyanobacterial communities were mostly composed of non-N-fixing cyanobacteria. There was only one case when TN:TP was greater than $150:1$ in which cyanobacteria were able to dominate in a lake (TN:TP = 371).

Question 3: comparative effects of land use, nutrients, and other factors on phytoplankton and cyanobacteria

We observed that in-lake nutrient concentrations were a better predictor of total phytoplankton and total cyanobacterial biovolume than any land use category predictor. Both TN and TP explained seven times more variation in total phytoplankton biovolume and two times more variation in cyanobacterial biovolume than did summed AD land use (Table 2). TN was the strongest predictor of total phytoplankton and cyanobacterial biovolume at the U.S. scale, as determined by AICc scores, and explained more variation in both phytoplankton biovolume ($R^2 = 0.38$) and cyanobacterial biovolume ($R^2 = 0.31$) than did TP (R^2 s = 0.37 and 0.28).

In contrast to total phytoplankton and cyanobacterial biovolume, AD land use contributed 2.5 times more variation in cyanobacterial dominance ($R^2 = 0.15$) than in-lake nutrients ($R^2 = 0.06$) at the U.S. scale. Again, TN and TP

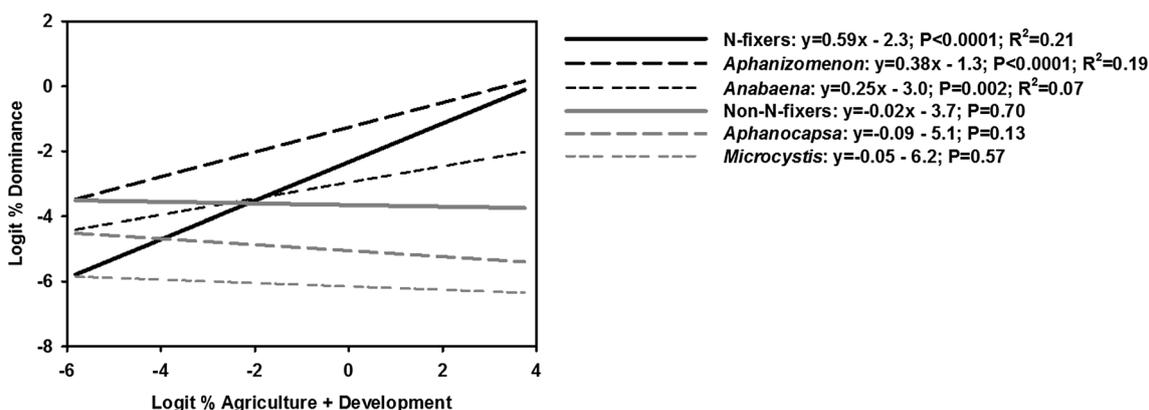


Fig. 4 Linear relationships between the dominance of N-fixing, non-N-fixing, and individual cyanobacterial genera vs. summed % agriculture and developed land use in a lake's perimeter across 236 lakes in the U.S. In general, aggregated N-fixing cyanobacteria (solid black line), which included *Aphanizomenon* (long-dashed black line)

and *Anabaena* (short-dashed black line) had positive, significant relationships with land use. Conversely, aggregated non-N-fixing cyanobacteria (solid grey line), which included *Aphanocapsa* (long-dashed grey line) and *Microcystis* (short-dashed grey line), exhibited no relationship with land use

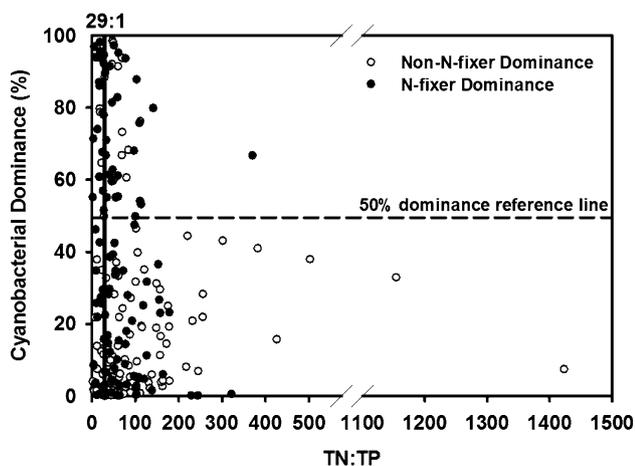


Fig. 5 The threshold of TN:TP that resulted in a large decrease in lake cyanobacterial dominance was about 150:1, approximately five times greater than Smith (1983)'s critical ratio of 29:1. Cyanobacteria were rarely dominant in TN:TP over 150:1 and when they were, it was mostly attributed to non-N-fixing genera. Black circles represent lakes that were dominated by N-fixing cyanobacteria and white circles were dominated by non-N-fixing cyanobacteria. The dashed line represents 50 percent dominance of cyanobacteria in the phytoplankton community. A break was inserted between TN:TP ratios of 550 and 1100 because no lakes were observed in this range

were both significantly and positively associated with cyanobacterial dominance ($P \leq 0.0002$ in both cases).

To determine the other effects of land use on phytoplankton communities in addition to TN and TP, we examined the relationship between AD land use and surface water temperature, which in turn may affect cyanobacteria. AD land use had positive significant effects on all three variables (TN, TP, and surface temperature; all $P \leq 0.0004$; Fig. 6; regression equations given in the figure), but lakeshore land use had a greater effect on surface

water temperature ($R^2 = 0.13$) than on TN ($R^2 = 0.06$) and TP ($R^2 = 0.05$). There was no significant relationship between AD land use and TN:TP (Fig. 6; $P = 0.12$).

Furthermore, surface water temperature was not significantly associated with total phytoplankton biovolume ($P = 0.27$). However, surface temperature was significantly and positively associated with cyanobacterial biovolume and cyanobacterial dominance ($P < 0.0001$ in both cases, $R^2 = 0.06$ and 0.08 , respectively). Lake depth and surface area were not significantly associated with surface water temperature (both $P > 0.05$).

Discussion

Here, we have shown that increasing levels of agriculture and developed land use across 236 naturally-formed lakes spanning the continental U.S. are positively associated with total phytoplankton biovolume, cyanobacterial biovolume, and cyanobacterial dominance. While these findings are not unexpected, our study augments and extends local and regional studies on the effects of land use on cyanobacteria (e.g., Hall et al. 1999; Katsiapi et al. 2012; Paul et al. 2012) to the continental U.S. scale.

Of the five anthropogenic land use categories, AD land use was the strongest predictor of cyanobacterial biovolume, cyanobacterial dominance, and N-fixing cyanobacterial dominance. AD land use and total agriculture were equally the strongest predictors for total phytoplankton biovolume. In concert, AD land use may stimulate cyanobacteria because of their complementary effects on nutrients and temperature that favor cyanobacterial dominance. Specifically, agricultural land use generally increases nutrient runoff into lakes (e.g., Sharpley et al. 1994;

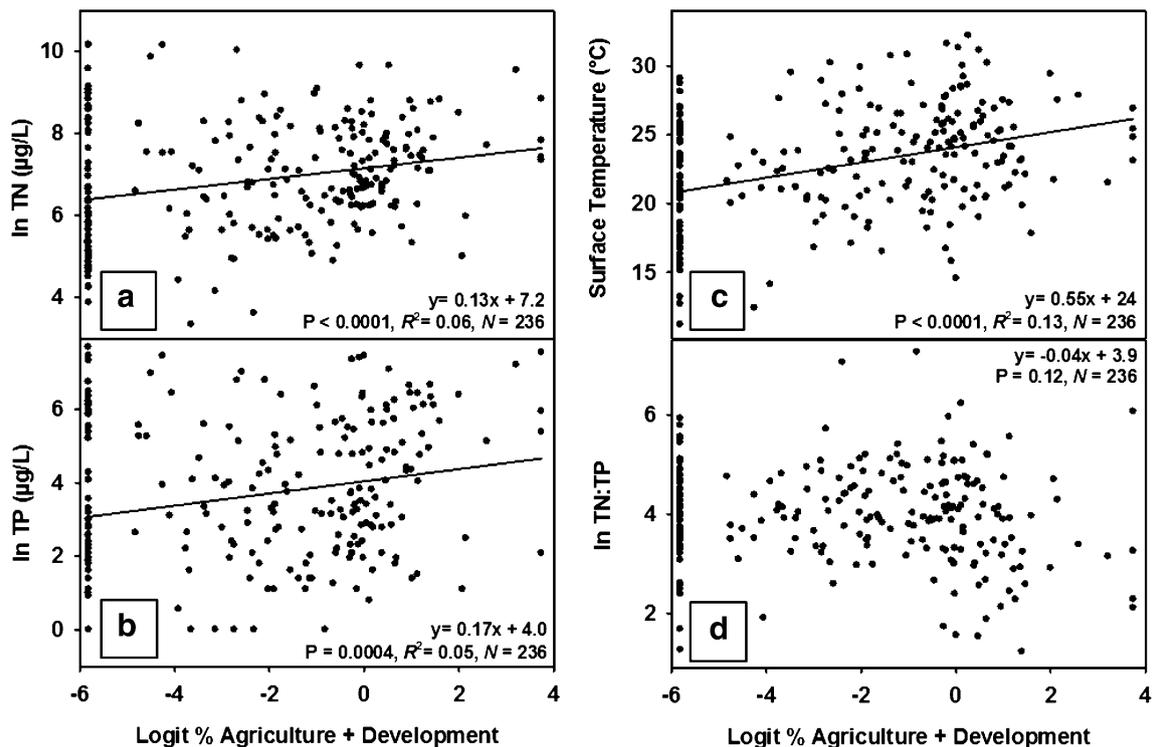


Fig. 6 Linear relationships of summed agriculture and developed land use and potential variables that may influence phytoplankton communities: **a** TN, **b** TP, **c** surface temperature, and **d** TN:TP

Carpenter et al. 1998; Vanni et al. 2011; Schindler et al. 2012), and developed land use may increase the temperature of water runoff as it enters lakes from impervious surfaces (LeBlanc et al. 1997; Fraterrigo and Downing 2008; Thompson et al. 2008a, b), or from warmer air-water temperature exchange (Otieno and Anyah 2012; Hu et al. 2015). While there is some debate as to whether increased nutrients or temperature is most important for driving cyanobacteria (Paerl and Huisman 2008; Brookes and Carey 2011; Rigosi et al. 2014), it is generally agreed that both factors together will promote cyanobacteria in lakes (Wagner and Adrian 2009; Kosten et al. 2012; Rigosi et al. 2014).

However, the positive association between anthropogenic land use and cyanobacterial biovolume and dominance at the U.S. scale was only qualitatively consistent in the Western Forested Mountains (ecoregion II) and the Nutrient Poor Largely Glaciated Upper Midwest and Northeast (ecoregion VIII). The other four ecoregions in the analysis exhibited largely positive, but non-significant, trends between cyanobacterial biovolume and dominance and anthropogenic land use. It is possible that these east and west coast ecoregions exhibited stronger relationships between land use and cyanobacteria because lakes in these ecoregions had overall lower mean anthropogenic lake-shore land use ($8 \pm 0.02\%$, 1 S.E.) to begin with, in

comparison to the other four ecoregions ($38 \pm 0.03\%$). For example, an initial conversion of land from completely forested (0% anthropogenic land use) to 10% anthropogenic lakeshore land use may have a greater influence on cyanobacteria than a comparable increase of anthropogenic land use when the watershed already has a considerable proportion (e.g., an increase from 40 to 50%). Following that reasoning, an initial pulse of land use conversion may be able to stimulate cyanobacterial increases in lakes, while that same numerical increase in anthropogenic land use may have a smaller effect on cyanobacteria in more developed watersheds. Because we do not have historical land use time series data for these lakes, we are unable to determine all of the reasons that contribute to these ecoregional differences.

Increased anthropogenic land use was also positively associated with the increased prevalence of several genera of N-fixing (and also toxin-producing) cyanobacteria such as *Anabaena*, *Aphanizomenon*, *Lyngbya*, and *Oscillatoria*. Conversely, there was no relationship between anthropogenic land use and non-N-fixing cyanobacteria, emphasizing the heterogeneity of cyanobacteria as a group, as cyanobacterial taxa with different eco-physiological characteristics (i.e., the ability to fix N) respond to anthropogenic factors such as land use and nutrients differently. We also found that N-fixing cyanobacteria were dominant

in the phytoplankton community up to a TN:TP ratio of $\sim 150:1$, about five times a previously reported molar ratio of 29:1 (Fig. 5; Smith 1983). Once a lake's TN:TP ratio exceeded 150:1, the cyanobacterial component of the phytoplankton community was primarily dominated by non-N-fixing taxa. This further emphasizes the heterogeneity of cyanobacteria as a group, as decreasing P runoff into a lake may not eliminate dominance by all cyanobacterial taxa, especially non-N-fixing genera such as *Microcystis*. Therefore, it would require a much greater reduction in P, or a greater TN:TP, to reduce overall lake cyanobacterial dominance.

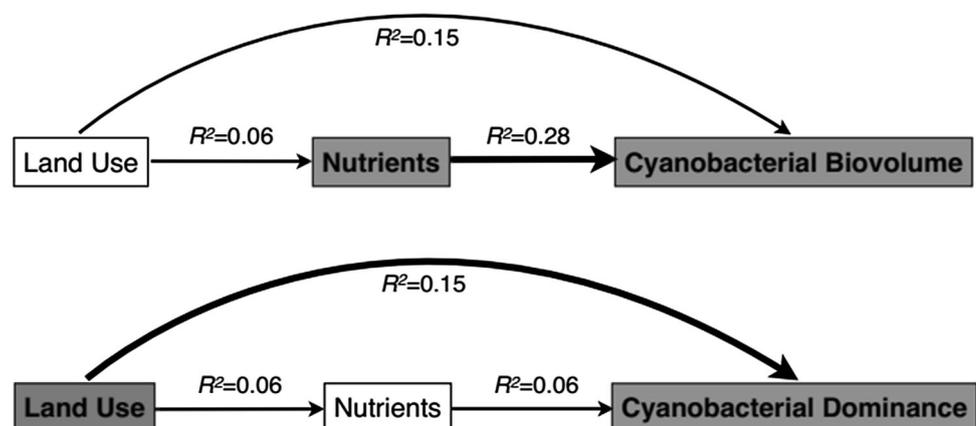
We observed a positive association between anthropogenic land use and lake TN and TP concentrations across the continental U.S., as expected from previous studies (e.g., Soranno et al. 1996; Gemesi et al. 2011; Wagner et al. 2011). TN and TP were stronger predictors for total phytoplankton and cyanobacterial biovolume, whereas land use was a stronger predictor for cyanobacterial dominance (Fig. 7). Therefore, other effects of anthropogenic land use than increased nutrient concentrations must also drive cyanobacterial dominance. We found that anthropogenic land use was positively associated with surface water temperature, and that surface water temperature was in turn positively associated with cyanobacterial dominance. Surface water temperature was neither associated with lake depth or surface area, suggesting that these lake morphology variables do not bias the relationship between AD land use and surface water temperature. However, we did not include climatic factors into our analyses, which could potentially confound results between land use and surface water temperature. Despite these limitations, we think the overall variation explained by surface water temperature by AD land use ($R^2 = 0.13$) is noteworthy considering the comparisons of lakes across the continental U.S., across regions of vastly different climates (e.g., temperate, highland, arid, and sub-tropical regions). Cyanobacterial taxa are generally better adapted to higher water temperatures

than other phytoplankton groups (Reynolds 2006; Paerl and Otten 2013; but see Lüring et al. 2013), likely increasing their dominance in lakes with warmer runoff coming from more impervious surfaces in the watershed. Surface water temperature, as well as other effects of land use, may play a role in why anthropogenic land use is a better predictor for cyanobacterial dominance than in-lake nutrient concentrations (Fig. 7).

One of the obvious limitations of the data used in this study is its temporal resolution. The EPA lake survey dataset had excellent spatial resolution for lakes across the continental U.S., but its temporal resolution was poor, with data collected only once or twice in a single year for each lake. Analyzing the data from a repeated sampling effort by the U.S. EPA NLA in 2012 will be helpful to see if the trends reported in this paper from 2007 are unique, or are consistent across multiple years. A second limitation of this study is that our conclusions only apply to natural lakes, not to man-made reservoirs. Factors unique to reservoirs, such as greater flushing rates and variable thermal stratification, confound associations of nutrients and temperature found in natural lakes (Wetzel 1990, 2001; Cooke et al. 2005; Beaulieu et al. 2013), which will be important to quantify in future studies.

Finally, one important limitation is the amount of unexplained variation in our study. It is perhaps not surprising for a dataset collected at such a large scale that much of the variation in phytoplankton community composition was left unexplained. This indicates that in addition to land use and nutrient variables, other factors, e.g., trophic structure and invasive species (Naddafi et al. 2007; White et al. 2011), or interactions among multiple variables (Hallegraeff 1993; Jöhnk et al. 2008; Rigosi et al. 2014), may be important determinants of cyanobacterial dominance that should be considered in future analyses. Given all of the possible within-lake and lakeshore land use factors that were associated with phytoplankton in the 236 lakes, however, it is still notable that anthropogenic land

Fig. 7 Conceptual diagram illustrating the strongest predictors for total cyanobacterial biovolume vs. cyanobacterial dominance. Nutrients (TN and TP) were the strongest predictor for total cyanobacterial biovolume. However, summed agriculture and developed land use was the strongest predictor for cyanobacterial dominance



use was able to explain up to 21 % of the variation in cyanobacterial dominance at the U.S. scale.

As the amount of variation in a phytoplankton metric explained by any single predictor variable aggregated to the U.S. scale was relatively low, it is likely that local to regional relationships may be more useful for water quality management. Examining the drivers of ecoregional variation should be a priority for deciphering regional to local level differences in water quality, as also suggested by others (Fraterrigo and Downing 2008; Dodds et al. 2009; Fergus et al. 2011; Wagner et al. 2011; Beaver et al. 2012). The continental-ecoregional comparison approach is a useful place to start in identifying potential drivers and application of water quality relationships across the U.S., but these U.S. scale relationships may be less relevant for local water quality management.

In an effort to control cultural eutrophication and its subsequent effects on increased cyanobacterial biovolume, significant research and policy initiatives have aimed to reduce nutrient loading, especially of P, into riverine and lake systems (Carpenter et al. 1999; Schindler 2012; Lehman et al. 2013). However, cyanobacterial biovolume is not necessarily the same variable as cyanobacterial dominance, as evident by their correlation ($r = 0.73$), which demonstrates that the two variables are strongly, but not perfectly, correlated. Hence, controlling only for the nutrient effects of land use may not reduce cyanobacterial dominance, even if biovolume decreases. We observed in this study that other effects of land use, such as increased surface water temperature, may also increase cyanobacterial dominance. Therefore, even in lakes with low cyanobacterial biovolume, blooms may still form if cyanobacteria are the dominant phytoplankton taxa (e.g., Carey et al. 2008, 2012b). Consequently, it is important to take into account both nutrients and the other effects of land use to control overall cyanobacterial biovolume and cyanobacterial dominance in lakes.

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