Outsized nutrient contributions from small tributaries to a Great Lake

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Excessive nitrogen (N) and phosphorus (P) loading is one of the greatest threats to aquatic ecosystems in the Anthropocene, causing eutrophication of rivers, lakes, and marine coastlines worldwide. For lakes across the United States, eutrophication is driven largely by nonpoint nutrient sources from tributaries that drain surrounding watersheds. Decades of monitoring and regulatory efforts have paid little attention to small tributaries of large water bodies, despite their ubiquity and potential local importance. We used a snapshot of nutrient inputs from nearly all tributaries of Lake Michigan—the world's fifth largest freshwater lake by volume—to determine how land cover and dams alter nutrient inputs across watershed sizes. Loads, concentrations, stoichiometry (N:P), and bioavailability (percentage dissolved inorganic nutrients) varied by orders of magnitude among tributaries, creating a mosaic of coastal nutrient inputs. The 6 largest of 235 tributaries accounted for ~70% of the daily N and P delivered to Lake Michigan. However, small tributaries exhibited nutrient loads that were high for their size and biased toward dissolved inorganic forms. Higher bioavailability of nutrients from small watersheds suggests greater potential to fuel algal blooms in coastal areas, especially given the likelihood that their plumes become trapped and then overlap in the nearshore zone. Our findings reveal an underappreciated role that small streams may play in driving coastal eutrophication in large water bodies. Although they represent only a modest proportion of lake-wide loads, expanding nutrient management efforts to address smaller watersheds could reduce the ecological impacts of nutrient loading on valuable nearshore ecosystems.

tributary | nutrient loads | Laurentian Great Lakes | eutrophication

Eutrophication arising from anthropogenic nutrient inputs has impaired lakes and reservoirs worldwide, leading to reduced water quality, altered ecosystem functions, and increased vulnerability to species invasions and harmful algal blooms (1–4). Following reductions in point sources of nutrient pollution since the 1970s, nonpoint sources have become the major drivers of eutrophication (5–7). Tributary streams and rivers are conduits from watersheds to receiving water bodies and are often focal points for directing on-the-ground nutrient management because they are strongly influenced by land cover patterns (8–10). Monitoring and regulatory efforts typically focus on the largest tributaries of lakes and marine coastlines because they dominate hydrologic inputs (hydraulic loads) and likely deliver the largest fraction of nutrients by virtue of their high discharge. Notably, the absence of consistent monitoring in small-sized and midsized watersheds has prevented understanding of the role that small tributaries play in overall nutrient delivery (11) and more importantly, local eutrophication along coastlines (12–15).

The Laurentian Great Lakes (hereafter Great Lakes) are a globally significant ecosystem that features the world's longest freshwater coastline (17,000 km), offering an ideal setting for examining tributary inputs to large water bodies. These lakes receive nutrients from thousands of watersheds that vary widely in attributes that affect the quantity and form of fluvial nutrients, including the presence of dams, stream order, catchment area, and land cover. The Great Lakes experience frequent algal blooms that have been linked to inputs from large tributary rivers, such as the Maumee River in Lake Erie, Fox River in Green Bay of Lake Michigan, and St. Louis River in western Lake Superior (16–19). These observations have fostered the expectation that large watersheds are responsible for the majority of watershed nutrient loading to the Great Lakes. As a result, almost all long-term monitoring of nutrient inputs in the Great Lakes is done on third-order rivers or larger, providing loading measurements for only the largest watersheds in the basin. For example, even though Lake Michigan has ~300 inflows (20), loads have been monitored for just 37 tributaries (21–23) and modeled for tributary inputs with watersheds >150 km^2 (8). Consequently, large tributaries have been prioritized for interventions to reduce nutrient inputs to the lakes. The lack of comparable monitoring of the abundant smaller tributaries yields substantial uncertainty about the overall magnitude, variability, and geography of aggregate nutrient inputs to the Great Lakes (11) and other large water bodies.

Given the surge in the number of freshwater ecosystems experiencing frequent and sustained algal blooms (3), a strategic approach is needed to direct management interventions toward

ENVIRONMENTAL SCIENCES

watersheds where load reductions are both feasible and likely to alleviate local eutrophication hot spots (15, 24). There are several reasons why nutrient inputs from smaller tributaries might warrant greater attention. First, small stream channels can have vastly different nutrient profiles than larger rivers (25–27). Second, after entering a receiving water body, plumes from small streams are more easily trapped in the littoral zone, thus increasing the likelihood that they will affect coastal ecosystem services (28). Third, overlapping plumes from multiple tributaries, which can occur readily among small tributaries with nearby inflows, magnify the adverse effects of watershed pollution on ecosystem services (29). Finally, while there are always challenges in implementing best management practices (BMPs) for nutrient control, they may be minimized in small watersheds with relatively simple land ownership patterns (30, 31). Thus, we posit that the lack of attention given to small-sized and midsized tributaries has led to overlooking important sources of nutrient loading and algal blooms in large receiving water bodies such as the Great Lakes.

The objectives of this study were to characterize total loads, yields (load per unit drainage area), and dominant forms of nutrients for every flowing tributary of Lake Michigan. Through this effort, we sought to evaluate the contribution that small tributaries make to lake-wide nutrient loads and which watershed characteristics drive variation among tributary inputs. We integrated measurements of total nutrient and dissolved inorganic nutrient concentrations with modeled discharge to estimate loading from nearly all perennial tributaries of Lake Michigan for a 6-d period in July 2018. Our snapshot approach at summer base flow was designed to maximize the spatial extent of sampling while minimizing confounding temporal variation, thereby elucidating spatial patterns of nutrient concentrations, bioavailability, loads, and yields across a wide range of tributary sizes and land uses.

Results

Gross Differences in Nutrients across the Tributary Size Spectrum.
Nutrient concentrations, stoichiometry (nitrogen [N]:phosphorus [P]), and bioavailability [defined here as the dissolved inorganic to total nutrient fraction (32)] varied by orders of magnitude among Lake Michigan's tributaries. Total nitrogen (TN) concentrations ranged from 0.22 to 9.53 mg N/L (Fig. 1A and *SI Appendix*, Fig. S1), ammonium ranged from below detection (<0.003 mg/L) to 1.05 mg N/L, and nitrate + nitrite varied from 0.003 to 9.48 mg/L. The proportion of TN composed of bioavailable dissolved inorganic nitrogen (DIN; nitrate + nitrite + ammonium) ranged from 1.8 to 100%. Total phosphorus (TP) concentrations varied from below detection (<0.003 mg/L) to 0.59 mg P/L (Fig. 1B and *SI Appendix*, Fig. S1), while soluble reactive phosphorus (SRP) ranged from below detection (<0.003 mg/L) to 0.53 mg/L. SRP represented between 2.7 and 100% of TP.

The vast differences in tributary nutrient profiles reflect spatial variation in land cover and watershed size (Fig. 2) and are also mediated by the presence of dams. TN and DIN concentrations both increased with agricultural and urban land fraction and decreased with watershed size, while TN increased slightly with wetland coverage (Table 1). The proportion of TN composed of DIN increased with percent agriculture and decreased as both watershed area and wetland percentage increased. TP concentrations were primarily driven by land cover, with agriculture, wetland, and urban coverage all leading to increased TP. SRP concentrations also reflected land cover differences, but there were multiple interactions among agricultural development, watershed size, and presence of dams (Table 1). Additionally, SRP increased with urban development and wetlands, regardless of watershed size or dams. Similar to DIN/TN, the proportion of TP composed of SRP increased with percent agriculture and decreased as watershed area increased. The differences in controls on TN and TP led to high spatial variability in tributary nutrient stoichiometry (N:P) (*SI Appendix*, Fig. S2), although several important relationships emerged. The N:P of tributary nutrients decreased (i.e., P was enriched relative to N) with percent urban or agricultural development and as watershed size increased. In contrast, presence of dams within watersheds increased tributary N:P.

Large Tributaries Deliver a Majority of Tributary-Derived Nutrients.
Tributary TN and TP loads were positively correlated with watershed area (Table 1), and several other watershed characteristics also influenced nutrient loads. Wetland extent and presence of dams within watersheds reduced TP load, and an
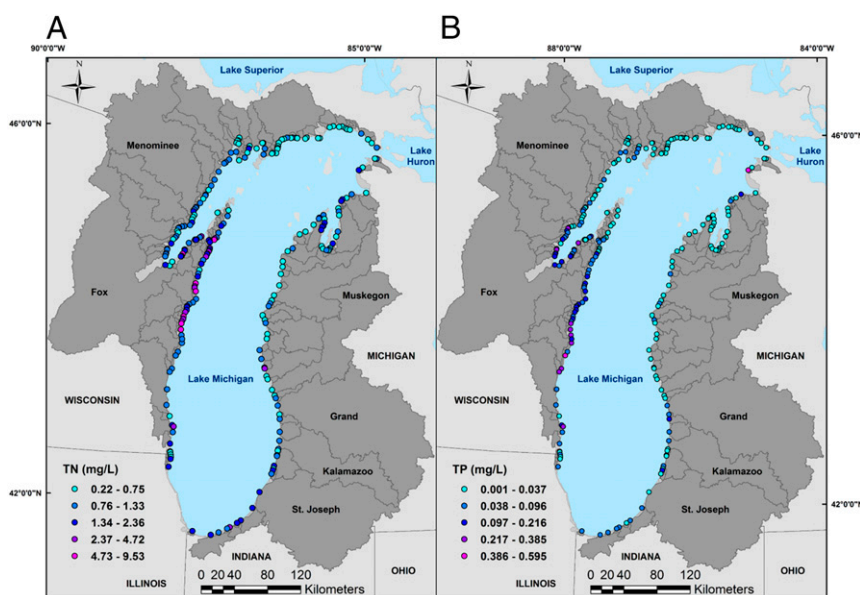
Fig. 1. TN (A) and TP (B) concentrations for the 235 tributaries sampled between 10 and 15 July 2018. The dark gray polygons represent sampled tributaries, and the unsampled tributaries, dry tributaries (no flow), and interfluve areas (regions in the basin that do not have a tributary outflow) are represented by light gray polygons. Capitalized labels represent several tributary watersheds, and state names are fully capitalized. The blue polygons represent Lake Michigan, Lake Superior, and Lake Huron.

interaction between agricultural development and watershed area suggested that the increase in TP load with watershed area is exacerbated by agricultural land use. TN loads decreased with wetland and urban extent, regardless of watershed size.

Small tributaries delivered only a modest fraction of the total tributary-derived nutrient load to Lake Michigan. Based on the sites we sampled, the comprehensive tributary TN and TP loads for Lake Michigan in mid-July 2018 were ~56.7 and 2.9 Mg/d, respectively. The six largest tributaries by watershed area (the Fox, the Grand, the St. Joseph, the Menominee, the Muskegon, and the Kalamazoo Rivers) (Fig. 1) accounted for nearly 70% of tributary-derived TN and TP (*SI Appendix*, Fig. S3). During this sampling period, the Fox River alone delivered 30% of the total daily TP load, and the St. Joseph River provided 28% of the total daily TN load. In contrast, the 184 sampled tributaries that drain watersheds <150 km² together accounted for less than 5% of the total tributary-derived TN and TP (*SI Appendix*, Fig. S3). Those same 184 tributaries were responsible for 7.6 and 8.3% of DIN and SRP daily loads, respectively.

The large disparities in watershed area among Lake Michigan's tributaries (<2 to over 16,000 km²) resulted in estimated discharges varying by four orders of magnitude. Even though nutrient concentrations varied by approximately two orders of magnitude, the much larger range in watershed area and discharge generally trumped the influence of land cover on loading rates. However, high N and P concentrations resulted in smaller tributaries (first to second order) having similar loads to midsized tributaries (third to fourth order), and there were numerous watersheds that produced comparable daily loads through disparate combinations of discharge and nutrient concentrations (Fig. 3). For example, high TN concentration in Lily Bay Creek (2.59 mg/L; 44°50′51.5580″, −087°16′03.7776″) led to delivery of the same 45-kg TN daily load as the Bark River (45°34′22.6380″, −087°14′36.3588″) from just 30% of the discharge.

Nutrient Yields Highlight Potentially Problematic Inputs from Small Tributaries. Like nutrient concentrations and loads, nutrient yields exhibited wide variation across Lake Michigan's tributaries. TN yields ranged from 0.03 to 3.65 kg/d per kilometer², and TP yields ranged from <0.001 to 0.64 kg/d per kilometer². TP yields decreased with wetland development and presence of dams (Table 1). Just as for TP loads, there was a positive interaction between watershed area and agriculture: TP yields decreased as watershed size increased, but the decrease in yield associated with larger watersheds was not as strong in watersheds with high agricultural land use. TN yields were negatively correlated with watershed size; smaller tributaries typically had higher TN yields than their larger counterparts. Additionally, TN yields decreased with wetland and urban extent, regardless of watershed size.

In parallel with comparing nutrient yields, we calculated TP and TN loading efficiencies (the proportion of aggregate tributary nutrient inputs relative to the proportion of aggregate tributary discharge) to assess which tributaries generate nutrient loads that are disproportionate to their hydrological inputs. We found that, in general, small tributaries with high nutrient concentrations deliver high TN and TP loads relative to their contribution to the lake-wide hydraulic load (Fig. 4).

Discussion

Despite the importance of rivers in fueling lake and coastal eutrophication, most monitoring and regulatory efforts have overlooked nutrient inputs from abundant small tributaries. Our July snapshot around the ~2,000-km perimeter of Lake Michigan gives insight into the important role that smaller tributaries have in coastal eutrophication in Lake Michigan and potentially, other large receiving water bodies. A few of the largest tributaries delivered a substantial majority of lake-wide nutrient loads, reflecting relatively high discharges from their expansive watersheds. However, we also found that small watersheds play a special role in nutrient loading through elevated nutrient yields, loading efficiencies, bioavailability, and N:P. These disparities suggest that nutrient inputs from small watersheds are likely to have outsized ecological impacts on the coastal zone by creating local hot spots of nearshore nutrients that could fuel algal blooms and eutrophication.

Differences in land cover, watershed size, and dams among watersheds all played significant roles in N and P dynamics of Lake Michigan's tributaries. Unsurprisingly, agricultural development was particularly influential—driving increased TP, TN, SRP, and DIN concentrations; bioavailability of N and P; and reduced N:P ratios. These are common patterns throughout the world, as use of land for intensive agriculture leads to increased particle-bound N and P (33), runoff of inorganic N and P from fertilizer application (25), and differential cycling of particulate vs. dissolved forms of nutrients (34, 35). The effect of agricultural development on SRP concentrations was mediated by watershed size and presence of dams, and our results suggest that the increase in SRP that occurred with agriculture is exacerbated in large watersheds but dampened by dams. We presume that this multilevel pattern reflects the greater probability of larger watersheds having large dams and the fact that river impoundment promotes processing and retention of nutrients—especially in agricultural watersheds (36). Urban land cover was associated with elevated TP, TN, DIN, and SRP, consistent with other
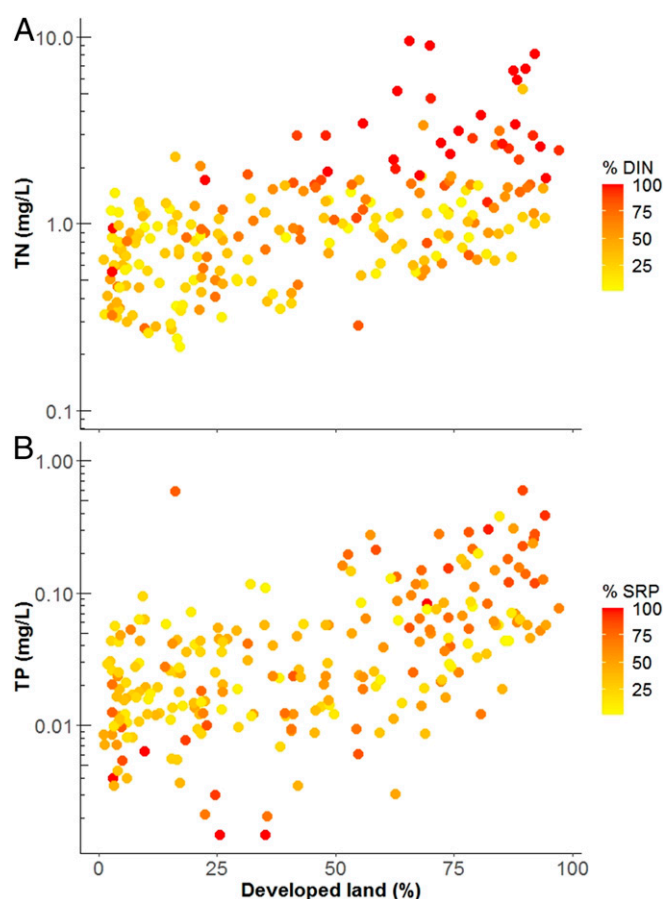

Fig. 2. Tributary TN (*A*) and TP (*B*) concentrations and the proportion of TN and TP composed of DIN and SRP (color of points), respectively. The 235 tributaries sampled between 10 and 15 July 2018 span a wide range of land development (combined agricultural and urban land cover).

Mooney et al.

Table 1. Multiple linear regression output for final models selected using backward Bayesian information criterion (BIC) model comparison

Nutrient metric (response variables) and main and interactive effects (independent variables)	Coefficient	SE	ΔBIC	R^2
TP (mg/L)				
Intercept	−2.18	0.098		
% agriculture	0.0125	0.001		
% wetland	0.0059	0.002		
% urban	0.0113	0.002		
Final model metrics			2.03	0.350
TN (mg/L)				
Intercept	−0.254	0.071		
% agriculture	0.0075	0.001		
% wetland	0.0025	0.001		
% urban	0.0045	0.001		
Area (km^2)	−0.0669	0.019		
Final model metrics			4.31	0.388
SRP (mg/L)				
Intercept	−2.4558	0.194		
% agriculture	0.0077	0.004		
Area (km^2)	−0.1333	0.116		
Dams present	−0.5406	0.294		
% wetland	0.0062	0.002		
% urban	0.0089	0.002		
% agriculture: area (km^2)	0.0060	0.003		
% agriculture: dams present	0.0193	0.007		
Dams present: area (km^2)	0.2105	0.155		
% agriculture: area (km^2): dams present	−0.0115	0.004		
Final model metrics			3.69	0.397
DIN (mg/L)				
Intercept	−0.6028	0.092		
% agriculture	0.0097	0.001		
% urban	0.0067	0.002		
Area (km^2)	−0.1918	0.041		
Final model metrics			4.72	0.273
% SRP of TP				
Intercept	44.25	3.914		
% agriculture	0.2945	0.057		
Area (km^2)	−5.4673	1.913		
Final model metrics			5.15	0.126
% DIN of TN				
Intercept	65.337	6.078		
% agriculture	0.189	0.079		
Area (km^2)	−9.631	2.202		
% wetland	−0.412	0.108		
Final model metrics			2.50	0.206
TP load				
Intercept	−1.751	0.103		
% agriculture	−0.0003	0.002		
Area (km^2)	0.925	0.055		
Dams present	−0.177	0.070		
% wetland	−0.003	0.002		
% agriculture: area (km^2)	0.005	0.001		
Final model metrics			5.23	0.820
TN load				
Intercept	0.023	0.060		
Area (km^2)	0.900	0.025		
% wetland	−0.006	0.001		
% urban	−0.004	0.001		
Final model metrics			2.59	0.861
TP yield				
Intercept	−1.751	0.103		
% agriculture	−0.0003	0.002		
Area (km^2)	−0.075	0.055		
Dams present	−0.177	0.069		
% wetland	−0.003	0.002		
% agriculture: area (km^2)	0.004	0.001		
Final model metrics			5.23	0.245
TN yield				
Intercept	0.023	0.060		
Area (km^2)	−0.099	0.025		
% wetland	−0.006	0.001		
% urban	−0.004	0.001		
Final model metrics			2.59	0.170
Molar N:P				
Intercept	2.169	0.077		
% agriculture	−0.003	0.001		
Area (km^2)	−0.130	0.042		
Dams present	0.158	0.073		
% urban	−0.005	0.002		
Final model metrics			3.13	0.102

Independent variables represent main and interactive effects in the final selected model for each response variable. ΔBIC represents the difference in BIC values between the final selected model and the more complex candidate model from backward selection.

Mooney et al.

studies that have shown urbanization can cause increases in most forms of N and P (35).

The fraction of TN and TP loads composed of DIN and SRP, respectively, shifted across the spectrum of tributary sizes, suggesting fundamental differences in nutrient processing between small and large rivers. Small rivers have shorter flow paths from land to water as well as within the channel, resulting in land use having stronger and more direct effects in small watersheds (27). In the specific case of agricultural watersheds, fertilizer-derived inorganic nutrients can travel quickly from land to stream to lake in smaller watersheds. Additionally, increased wetland coverage within a watershed tended to decrease the fraction TN composed of DIN, which could be due to increased denitrification in wetland sediments that permanently removes inorganic N (37). Our results suggest that variation in anthropogenic land development and watershed size have important roles in mediating nutrient dynamics among coastal inputs, especially for water bodies with hundreds of highly variable tributaries.

The disparities in N and P loading profiles among watersheds of Lake Michigan are likely to create a mosaic of algal communities and eutrophication risk along the coast. Across tributaries, total nutrient concentrations spanned the range associated with the oligotrophic–eutrophic spectrum of ecosystem productivity (38), while N:P ranged from values indicating extreme N limitation to extreme P limitation for algae in freshwater ecosystems (39, 40). There were also sharp differences in nutrient bioavailability (Fig. 2). Collectively, tributary inflows could create local variation in algal communities along the coastline by shifting the relative availability of different nutrients, thereby granting competitive advantage to particular taxa (41, 42). For example, N-fixing cyanobacteria typically dominate in low N:P waters when P concentrations are relatively high (43). Some stretches of the coast received inputs from multiple watersheds with similar nutrient profiles, but other regions featured adjacent tributaries that were markedly different. For example, there are only 4 km of coast between the three rivers (the Ogontz, the Little, and the Big Rivers) that flow into Ogontz Bay in Michigan (45°51′20.4264″, −086°45′28.3752″), yet their TN and TP concentrations varied by an order of magnitude, and the dissolved proportions of TN and TP ranged from 7 to 29% and from 13 to 82%, respectively.

The diversity of nutrient conditions expected to arise around the mouths and adjacent shorelines of these hundreds of tributaries surely extends the range of nutritional environments available to algae and microbes. In this way, tributaries may support niches that enhance aggregate ecosystem biodiversity. Although we usually conceptualize large water bodies as stable environments compared with the flow and thermal variation of tributaries, the diversity of river mouth conditions could in fact offer ecological refugia as prevailing conditions in the lake fluctuate seasonally. In that scenario, specialized taxa that are sustained by local tributary inputs could become the foundation for blooms whenever favorable conditions arise within the larger water body. Although speculative, the diversity of environmental conditions engendered by differences in tributary inputs represents an important ecological extension of our findings.

Due to their increased dissolved inorganic nutrient concentrations, smaller tributaries made a greater contribution to the lake-wide loads of DIN and SRP (~7.6% of DIN and 8.3% of SRP) compared with TN and TP (~4.8% of TN and 4.0% of TP). Particulate and organic N and P become available to primary producers only after mineralization or other transformations (44), and as much as 70% of particulate nutrients may be deposited and permanently buried in lake sediments rather than becoming bioavailable (45). Thus, tributaries that deliver water with either greater concentrations of dissolved inorganic nutrients or a higher fraction of nutrients in bioavailable forms are more likely to produce nearshore algal blooms during the summer growing season (19). While other factors also affect localized coastal nutrient

availability and eutrophication risk within Lake Michigan and the other Great Lakes, such as littoral nutrient retention by invasive dreissenid mussels (46, 47) and rising water temperatures (19, 48), bioavailable nutrient inputs often serve as an essential trigger for coastal eutrophication, especially in summer (49). Synergies among these various influences are likely to mediate coastal eutrophication; hence, understanding the geography of highly bioavailable nutrient inputs in conjunction with other spatially and temporally variable drivers represents a critical frontier in efforts to conserve valuable coastlines (50).

The ecological consequences of nutrient inputs across the size spectrum of tributaries may be further amplified by coastal mixing processes. The hydraulic power of high-discharge plumes from large rivers enables them to transport their nutrient load further offshore than smaller inflows. Small plumes typically lack the coherence and momentum to reach the pelagic zone and instead, are retained along the shoreline (51). Because inflows from small tributaries tend to get trapped near shore and have high total and inorganic concentrations of N and P, these small systems should be particularly effective at locally fertilizing the coast. Given that the littoral zone is a hot spot for both human–lake interactions (52, 53) and aquatic biodiversity (54), tributary loads that differentially affect nearshore water quality are particularly concerning. Further, lake physics can strongly mediate the distribution of tributary-derived pollution from watersheds. When lake hydrodynamics cause tributary plumes to be trapped and intermingled, the detrimental effects on coastal water quality and ecosystem services could be magnified (29).

Focusing on aggregate nutrient loading rates has made it easy for environmental management to overlook small watersheds, but our findings reveal a need to reconsider these systems due to their outsized biological and ecological effects on the coastal zone. Prioritizing watersheds with high nutrient yields (Fig. 3) or whose contribution to lake-wide loading is disproportionately large relative to their hydrological input (Fig. 4) would identify opportunities for strategic nutrient load management. BMPs, such as cover crops and wetland restoration (55), are often applied successfully and with high return on investment in small, high-yielding watersheds (56–58). This logic is implicitly embraced when BMPs are targeted toward high-yielding subcatchments nested within larger, high-loading tributaries (i.e., the Fox River of Lake Michigan and the Maumee River of Lake Erie) in an attempt to reduce their loads. Our results suggest that extending this approach by applying BMPs to smaller watersheds that flow directly into large water bodies could offer a cost-effective means of reducing local eutrophication engendered by inputs of highly bioavailable nutrients.

Our snapshot of tributary nutrients provides the most spatially comprehensive view of nutrient loading available for a large water body but has important limitations. We used extensive one-time sampling to ensure that load estimates among tributaries were comparable in terms of seasonal inputs and discharge dynamics. This level of temporal control comes at the cost of missing high-flow events that produce substantially higher loading rates in short pulses (59). To put our snapshot into perspective, the Fox River in Wisconsin has some of the largest annual nutrient loads to Lake Michigan at 5,000,000 kg TN and 400,000 kg TP per year (8), but a simplistic extrapolation of our 1-d summer estimate to the entire year represents only 60 and 75%, respectively, of the actual annual load. Thus, our estimates should not be treated as proxies for annual loads. Additional complexity could arise from disparities in hydraulic and nutrient load responses to storms due to watershed size or parent geology. The six largest tributaries accounted for ~52% of aggregate discharge to Lake Michigan during our summer assessment period but would contribute ~61% of all water flow if all sampled tributaries were flowing at their respective maximum discharge during 2018. Additionally, spatial variation in geology creates differences in soil depth and hydraulic conductivity that
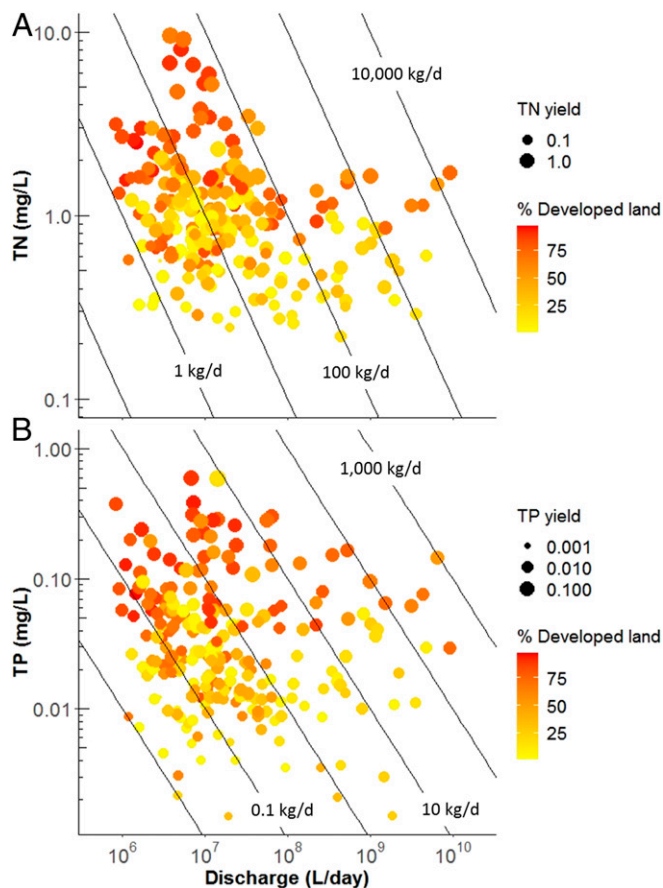
Fig. 3. Combinations of discharge (liters per day) and TN (*A*) and TP (*B*) concentrations responsible for estimated daily nutrient loads for 235 tributaries of Lake Michigan between 10 and 15 July 2018. Contour lines indicate TN or TP loading rates (kilograms per day) of the same order of magnitude. Point size is scaled to nutrient yield (kilograms per day per kilometer^2), and point color represents the fraction of watershed area that has been developed (combined agricultural and urban percentage).

shape watershed flow paths and thus, the movements from land to stream (60–62). While complex interactions among land cover, geology, and stream chemistry are challenging to identify with synoptic sampling (63), especially when geological properties are highly collinear with land cover (*SI Appendix*, Fig. S5), such effects might emerge in response to different hydrologic conditions and have differential effects on bioavailability or amounts of N and P delivered to the lake (63–65).

Our approach sacrificed temporal representation in favor of spatial representation to gain insights into the watershed correlates of nutrient inputs, with the premise that disparities in nutrient loads and yields across tributaries of large water bodies are poorly known compared with well-documented statistical distributions of daily loads and discharge through time (66, 67). Our results reveal that nutrient loads vary even more widely than discharge across the spectrum of tributary size, thereby complementing well-known patterns of temporal variation in loading from watersheds of any given size. There is surely much to learn from testing how the spatial patterns illustrated here shift with time in response to seasonal precipitation and storm events. Such spatiotemporal integration will be necessary in order to fully resolve the role of small tributaries in coastal nutrient dynamics along the extensive coasts of large lakes and oceans.

Reducing inputs of nutrients to sensitive coastal environments remains a key management priority worldwide, particularly where harmful algal blooms and other symptoms of cultural

eutrophication are evident (15, 68–70). Our findings indicate that efforts to control coastal nutrient loading could be enhanced by looking beyond the largest watersheds. Although aggregate tributary inputs of N and P are dominated by large rivers, we expect outsized ecological consequences of loading from small-sized and midsized tributaries due to their combination of increased dissolved inorganic nutrients, greater bioavailability, limited capacity to transport their loads away from the shoreline, and likely overlaps of plumes from nearby streams. Small watersheds may also be more feasible targets for management interventions because they are overseen by fewer land owners and political jurisdictions, on average, than larger counterparts (31). To help protect the irreplaceable ecosystems services from the Great Lakes—such as $15 billion annually from drinking water, recreation, fisheries, and shipping (52, 53)—hundreds of watershed organizations have mobilized to seek environmental improvements in their own backyard (71). Such vested interests and collective influence of citizens and communities have the capacity to improve local management of nutrients and advocate for healthy coastal ecosystems. Our results suggest abundant opportunities to advance lake-wide management goals by addressing nutrient loading from small watersheds of Lake Michigan, and this model is likely to be applicable to many other large freshwater and marine ecosystems.
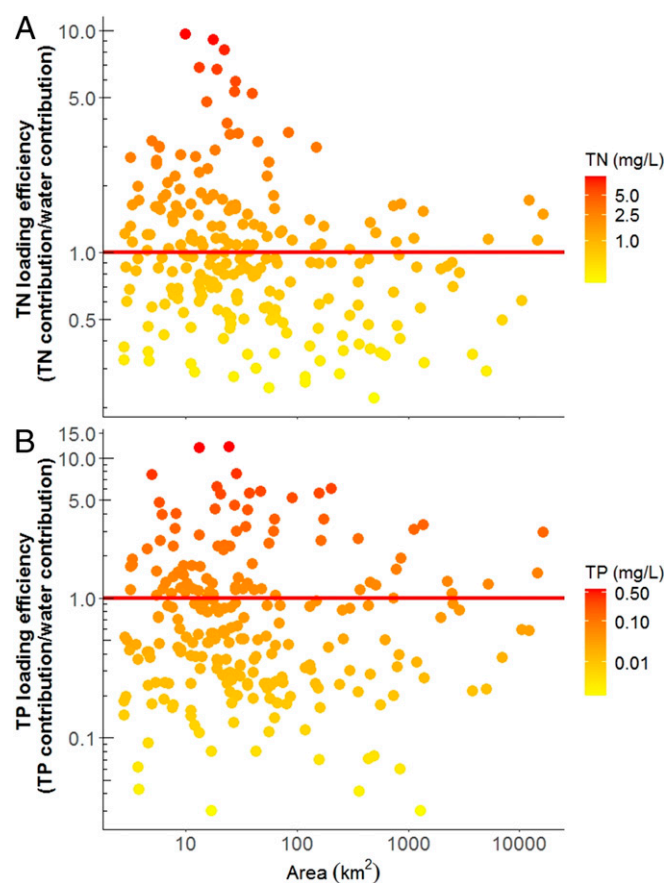

Fig. 4. Scatterplot for 235 tributaries sampled between 10 and 15 July 2018 showing ratios between the contribution that individual tributaries made toward the lake-wide N (*A*) or P (*B*) load with its contribution to the lake-wide hydraulic load. The horizontal red lines represent a ratio of one, where the nutrient load is directly proportional to the hydraulic load. Colors of points represent tributary TN (*A*) or TP (*B*) concentrations (milligrams per liter).

Methods

Study System. The Lake Michigan Basin provides an ideal ecosystem to estimate comprehensive nutrient loads and determine the spatial variability of nutrient profiles across the tributary size spectrum. The basin captures a wide range of tributary watershed size and land covers (*SI Appendix*, Fig. S4) found in the Great Lakes region, from undeveloped northern watersheds to highly urbanized areas, with variable amounts of agriculture across the natural–urban spectrum. The size of the basin paired with its high development results in Lake Michigan having the second highest total nutrient input of all of the Great Lakes, second only to Lake Erie (8). Lake Michigan's approximate 294 tributaries range from small, first-order streams with catchments of just 3 km^2 to sixth-order rivers with catchments as large as 16,000 km^2. Over 250 of its tributaries are first-, second-, or third-order streams with areas of 150 km^2 or less (20).

Tributary Water Collection. Between 10 and 15 July 2018, we sampled 235 of Lake Michigan's 294 tributaries. All sampling took place under low- to moderate-flow conditions when streams were below their 30th percentile of discharge for 2018. We visited an additional 26 tributaries that were not flowing and thus, not contributing to the total nutrient input during the sample period (but may during times of the year with higher discharge). We were unable to sample 33 tributaries (which accounted for ~3% of the lake's basin) that were inaccessible for various reasons. Surface water was collected at the road crossing nearest to the mouth via bridge sampling methods (72). Collected water was left unfiltered for TN and TP analyses or immediately filtered through a 0.45-μm glass fiber filter for DIN and SRP analyses. All samples were kept on ice in the field and frozen within 10 h of collection. Water samples remained frozen until nutrient analyses were performed.

Nutrient Analyses. SRP and DIN concentrations were determined for all filtered water samples using an Astoria-Pacific Astoria II segmented flow autoanalyzer and standard colorimetric assays (73). TP and TN were determined using similar methods following a persulfate digestion. Specific protocols can be found at https://lter.limnology.wisc.edu/research/protocols. If dissolved nutrient concentrations exceeded measured total nutrient concentrations, we assumed the discrepancy was due to sampling or measurement variability and assumed that all nutrients were in the dissolved form.

The detection limit for TN was ~0.021 mg/L, and the analytical range for the method extends to 2.5 mg/L. The detection limit for ammonium was ~0.003 mg/L, and the analytical range for the method extends to 4.0 mg/L; the detection limit for nitrate + nitrite is ~0.002 mg/L. For TP and SRP, the detection limits were 0.003 mg/L. Samples that extended beyond the maximum of each method were diluted until they were within the detectable range. Concentrations that were below detection limit were adjusted to half of the detection limit concentration of each analyte. Although this may not be the most accurate way to adjust low concentration samples, it seemed appropriate given the wide range of concentrations that occurred across our sample set.

Discharge Estimates and Load and Yield Calculations. Discharge was estimated for each sampling point location by the discharge-area ratio method. First, all US Geological Survey (USGS) stream gauges within the US Great Lakes Basin states with at least 20 y of recorded data were downloaded, resulting in 3,997 stations. From these, a geographic information system (GIS) feature was created using the latitude and longitude from each stream site. The gauges were then subset by those with a reported drainage basin area and intersected with an outline of the US Great Lakes Basin. Following intersection, 924 gauged streams in the Great Lakes Basin remained. Daily discharge data for all gauges were then downloaded from the USGS National Water Information Service using its Representational State Transfer Application Programming Interface (REST API) coded within MATLAB for the period 1980 to 2018. From the 924 gauges within the Great Lakes Basin with reported catchment areas, 657 had discharge data within this time window. Discharge values were then binned into 5-d averages and divided by basin area to compute 5-d basin yield averages (runoff). These basin yield values were interpolated to our coastal sampling locations using a two-step interpolation procedure. For each binned period, basin yield values were first

interpolated using nearest-neighbor linear interpolation. This method allowed extrapolation beyond the convex hull of observed basin yield locations but can sometimes produce spurious values due to both extrapolation and having too few nearby gauges. In those instances, a secondary interpolation using nearest neighbors was used. Finally, the interpolated basin yield values above or below observed minimum and maximum values were truncated. Following interpolation of basin yield, each sampling location was then multiplied by its catchment area to compute 5-d average discharge.

To validate this approach, we subset the 657 gauges into validation and observed subsets and predicted discharge at the validation locations using the observed location values. For this separate validation, 10% of the 657 gauges were selected as a validation subset, with the remaining 90% as observed values. The median root mean square error (RMSE) of the 5-d average predicted discharge across the 65 validation sites was 11.0% of observed flow at each location. For 25% of sites, the RMSE was less than 5.02% of discharge, while at the high end of error, 25% of sites had RMSE values greater than 23.6% of discharge. We used this validation procedure to select the discharge averaging period. For bin widths greater than 5 d, discharge prediction error did not appreciably decrease, while for shorter periods, discharge prediction errors increased significantly. This is the case because as this procedure uses time-varying basin yield values from a range of gauged catchment sizes, temporal responses to precipitation or snowmelt events can vary significantly. Below 5 d, this source of error dominates discharge estimation. For ≥5 d, the short-term responses to precipitation events are averaged out, and instead, error is dominated by differing land cover, soils, slopes, groundwater conditions, and other hydrogeological characteristics that vary across catchments.

Nutrient loads were calculated as the product of concentrations and discharge estimates. Discharge was represented by the 5-d mean around the actual sampling date for each tributary. Yields were calculated by dividing the nutrient load by the area of the corresponding watershed.

Spatial Data and Statistical Analyses. Watershed area was determined using the Great Lakes Aquatic Habitat Framework database (74), and presence of dams within watersheds was determined using the spatial database from Januchowski-Hartley et al. (75). Land cover proportions were determined using the National Land Cover Database for 2011 (76).

All data met assumptions of parametric tests (after log_{10} transformation, in the case of nutrient loads, yields, concentrations, and watershed area). Multiple linear regressions were used to determine if land cover types (percent agriculture, percent urban, and percent wetland), watershed area, and presence of dams along the tributary had main effects and/or interactive effects on TN and TP loads and yields; TN and TP concentrations; DIN and SRP percentages of TN and TP, respectively; and molar N:P. Forest land cover was removed prior to analyzing regression models to reduce collinearity among main predictor variables and ensure that the variance inflation factors were acceptable. Multiple linear regression models were selected using backward Bayesian Information Criterion (BIC) model comparisons to ensure that our final models were parsimonious. All final models had a ΔBIC greater than two. However, if the two most reduced models for a nutrient metric had a ΔBIC < 2, we reported the more complex model, which occurred for TN concentration, TP load, TP yield, and N:P stoichiometry. We chose this approach because all models with ΔBIC < 2 are often considered to be similar, and the more complex model has support to be considered as the final model (77–79). All statistical analyses were completed in R v. 3.2.2.

Data Availability. All data files and R analytical scripts/code used in this manuscript have been deposited in GitHub (https://github.com/RobertJMooney/LMtribs).

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