Physiographic gradients determine nutrient concentrations more than land use in a Gulf Slope (USA) river system

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Abstract: Riverine ecosystems are linked to their watersheds, and both land use and physiographic environmental conditions influence nutrient dynamics and water quality. We assessed aquatic nutrients and their relationship with land use and physiographic conditions at multiple spatial scales in the Brazos River watershed (Texas, USA) to examine the interactions between land use and physiography and their combined influences on riverine nutrient dynamics. Patterns in physiography and land use were highly correlated, but physiographic gradients explained ~2× more of the variability in riverine nutrient concentrations than land use (25 and 12%, respectively). The response of nutrient concentrations to spatial patterns of land use and physiography depended on the specific nutrient and scale of analysis. However, elevated dissolved nutrient concentrations typically were associated with areas of higher rainfall, greater stream density, and more intensive human alteration of the catchment. In contrast, particulate nutrients were more responsive to catchment area and seasonality. Seasonality and reach-scale % rangeland had the strongest independent effects on concentrations of particulate nutrients, whereas the specific ecoregion type and catchment-scale % urban use had the strongest independent effects on dissolved nutrients. Our study highlights the importance of incorporating physiographic environmental gradients when studying the interactions between a river and its watershed, especially in large, complex watersheds or those that cross steep environmental gradients.

Key words: nutrients, land use, riverine, environmental gradients, agricultural streams, urban streams

Rivers transform, process, and transport nutrients to downstream ecosystems, thereby supporting important ecosystem functions and providing valuable ecosystem services (Costanza et al. 1997, Thorp et al. 2010). Lotic ecosystems are networks that link upland terrestrial ecosystems to downstream aquatic regions (Allan 2004, Thorp et al. 2010). Human landscape development has occurred without consideration of the effect on riverine systems and, thus, threatens the ecological integrity of many river systems (Allan 2004). In the USA, the leading sources of impairment to river systems usually are agriculture in the watershed or hydrologic modification (USEPA 2009), but critical gaps exist in our knowledge about riverine ecosystem ecology and function, and their linkages to terrestrial landscapes (Allan 2004).

Landscape features that link aquatic to terrestrial systems include patterns of land use/land cover (LULC) and physiographic environmental variables (e.g., climate and geomorphology). The effects of these patterns are complex (Allan 2004, King et al. 2005). The influence LULC variables, such as % agriculture in a watershed or presence of riparian buffer strips, on ecosystem variables can differ among variables (e.g., in-stream NO_3^- vs soluble reactive P [SRP] concentration; Dow et al. 2006) or scales of analysis (e.g., riparian zone vs whole watershed; Dodds and Oakes 2006). Studies of the effects of LULCs on nutrient concentrations in lotic systems often focus on high-impact LULCs, such as urban and agricultural land use in the watershed (Dodds and Whiles 2004, Sonoda and Yeakley 2007). However, the strength of this linkage varies with stream order and watershed size (King et al. 2005, Dodds and Oakes 2008), and spatial covariation between natural and anthropogenic environmental drivers can complicate interpretation of the relationships between LULC and water quality (Allan 2004). For example, regional geology can determine suitability of areas for agriculture and

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can influence stream nutrient concentrations (King et al. 2005, Dow et al. 2006). Thus, we need to move beyond questions about patterns of LULC and the spatial scales at which these patterns most influence riverine ecosystems to questions that address the covariation between physiographic and land use patterns.

The degree of covariation between LULC and physiographic context is rarely addressed (but see Dow et al. 2006), and most researchers focus primarily on the influence of LULC patterns on water quality (Allan 2004). Moreover, most studies are conducted on relatively small watersheds that lack a substantial range of physiographic environmental gradients (Sliva and Williams 2001, Dodds and Oakes 2006, Dow et al. 2006). In large watersheds, use of physiographic environmental predictors allows examination of the interactions of LULC with naturally occurring environmental gradients in the watershed (Goldstein et al. 2007). Physiographic environmental variables are sometimes a component of riverscape studies (Sliva and Williams 2001, Dodds and Oakes 2008), but, to our knowledge, the only study in which the investigators partitioned out the effects of LULC and a covarying set of predictors are Dow et al. (2006), who found that the influence of LULC patterns was greater than that of geologic factors.

We examined the combined and individual influences of physiographic environmental gradients (e.g., location, ecoregion, slope, or stream density) and LULC patterns and the degree to which these large-scale and relatively static factors influenced nutrient concentrations in the Brazos River, Texas (Gulf Slope, USA). We hypothesized that: 1) physiographic and LULC gradients would overlap substantially in the Brazos River watershed, but that LULC variables would have a greater influence than physiographic gradients on water quality and nutrient concentrations; 2) effects of LULC would be stronger at the reach (100-m riparian buffer to 2 km upstream) and riparian (100-m riparian buffer portion of entire upstream watershed) scales than at the catchment scale (the subwatershed above a site), but the predominant scale and strength of influence would depend on the specific nutrient and season; and 3) land uses associated with intense modification (e.g., % urban use or % agricultural land) would exert the strongest influence on in-stream nutrient concentrations (King et al. 2005, Dow et al. 2006).

METHODS

Study site and sampling design

The Brazos River spans 2060 river km from its source near the Texas–New Mexico border to the Gulf of Mexico. We focused on the lower ⅓ of the watershed, which has an area of ~41,000 km^2 (Fig. 1). The main-stem of

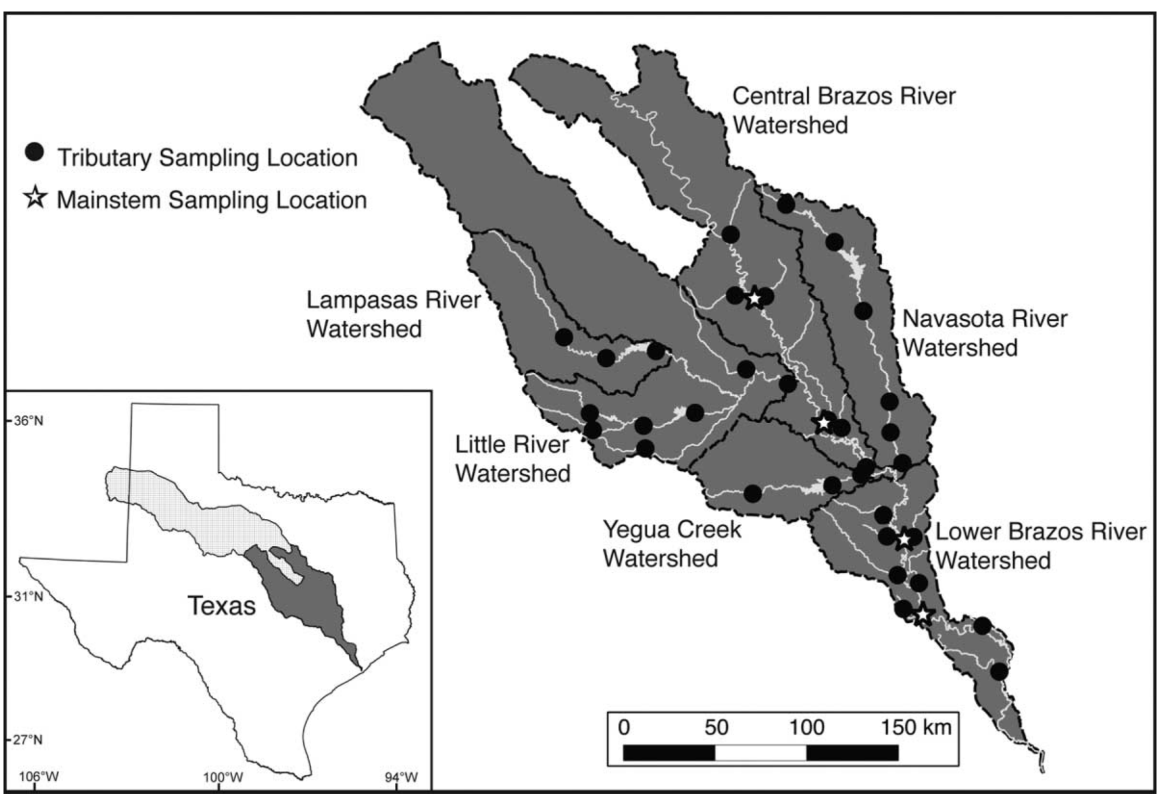

Figure 1. Sampling sites and study catchments in the Brazos River watershed, Texas. Inset shows the entire Brazos River watershed. Light stippling indicates the upper Brazos watershed; grey area indicates focus of our study.

the river is free of impoundments in the study area, but the river upstream and its major tributaries are regulated by dams (Zeug and Winemiller 2008). Our study area encompassed 4 ecoregions: the Edwards Plateau (EDPL), Texas Blackland Prairie (TBPR), East Central Texas Plains (ECTP), and the Western Gulf Coastal Plains (WGCP). We sampled 33 sites across the lower Brazos watershed (Table S1). Sites were situated along a combination of independent small tributaries and major tributaries, including the Navasota, Yegua, Little, and Lampasas Rivers. We also sampled 4 sites along the main stem of the Brazos River that were influenced by the physiographic conditions and LULC throughout the entire watershed above each site (Fig. 1, Table S1). We collected water samples in duplicate from all sites in 3 field seasons during 2008–2009. Spring sampling occurred from March to May 2008, summer sampling occurred from June to August 2008, and winter sampling occurred from November 2008 to January 2009.

We analyzed LULC patterns and scalable physiographic variables at 3 spatial scales (sensu Allan 2004): 1) reach-scale = the LULC in a 100-m buffer strip on each side of the channel for a 2-km linear distance upstream from the study site; 2) riparian-scale = the intermediate-scale LULC in a 100-m buffer-strip on each side of the channel for the entire extent of the watershed upstream of the study site; and 3) catchment-scale = the large-scale land use pattern across the entire watershed upstream of the study site. To keep our terminology consistent with Allan (2004), we use 'catchment' when we are referring to part of our analysis and 'watershed' as a more general term. At each site, we calculated landscape maximum slope, mean slope, and standard deviation of slope (a measure of slope variability appropriate for low gradient watersheds; Sliva and Williams 2001) in ArcInfo 9.3 (Environmental Research Systems Institute, Redlands, California), and the nonscalable variables, stream density (stream length/catchment area, km/km^2), catchment area (km^2), latitude, and longitude (in decimal degrees) as physiographic variables. We used season as a physiographic variable because seasonal patterns in meteorological variables and river discharge depend on physical location within a watershed (Petersen et al. 2012). Season and US Environmental Protection Agency Level-III ecoregions were categorical physiographic predictor variables. Including site latitude, longitude, sampling season, and ecoregion enabled us to incorporate the effects of spatial and temporal structure in the data in the analyses.

We extracted data for LULC, elevation, stream networks, ecoregions, and average rainfall from US government databases (Table S2). All geographic information system (GIS) analyses were conducted with ArcInfo 9.3. We delineated the catchments with ArcHydro (Maidment 2002) in ArcInfo. Raw LULC data had a 30-m resolution and contained 21 LULC classes. We reclassified data based on Anderson et al. (1976) Level-I classes, which resulted in 7 LULC categories: urban use, cultivated land, forest, rangeland (including grasslands), wetland, open water, and barren land. Barren land (e.g., exposed rock or strip-mining areas) was removed from analysis because it gen-

Table 1. Watershed, ecoregion, physicochemical, and land use/land cover (LULC) data and abbreviations.

Variable	Abbreviation	Variable	Abbreviation
Watershed		Ecoregion	
Central Brazos River	CW	East Central Texas Plains	ECTP
Lampasas River	LM	Edwards Plateau	EDPL
Little River/San Gabriel River	LR	Texas Blackland Prairie	TBPR
Lower Brazos River	LB	Western Gulf Coast Plains	WGCP
Main stem Brazos River	MS	Land use/land cover	
Navasota River	NR	Cultivated land (% cover)	Ag
Yegua Creek	YG	Forest (% cover)	For
Physicochemical Data		Open water (% cover)	O.W.
Latitude (decimal °)	Lat	Rangeland (% cover)	Ran
Longitude (decimal °)	Long	Urban use (% cover)	Urb
Catchment area (km^2)	C.Area	Wetland (% cover)	Wet
Mean annual precipitation (cm)	MAP	Scalable variables	
Mean slope (% grade)	MSlp	Reach scale	1
Max slope (% grade)	MxSlp	Riparian scale	2
Standard deviation of slope (% grade)	sdSlp	Catchment scale	3
Stream density (km/km^2)	StrDen		

erally constituted <1% of the total area in the study region (Dodds and Oakes 2008). We used digital elevation models (DEMs) at 1-arc-second (~30-m) resolution to delineate watersheds and calculate slopes. We derived stream density from the stream network and DEM-derived watershed delineation data. We assigned sites to EPA Level-III ecoregions of Texas (USEPA 2012) to incorporate broad patterns of geology, soil structure, and vegetation in the analyses. We calculated 30-y average rainfall for each site with data from the Texas Water Development Board.

Stream sampling and laboratory analyses

We measured water temperature (°C), dissolved O_2 (DO; mg/L), specific conductance (μS/cm), and pH at each site with YSI® sondes (models 556 or 85; Yellow Springs Instruments, Yellow Springs, Ohio). We collected water in acid-washed 2-L brown Nalgene® bottles rinsed with site water before sample collection. We kept bottles cold and processed samples within 48 h of collection. In the laboratory, we analyzed samples immediately or divided them into subsamples, which we preserved for future analysis. We measured total N (TN), total P (TP), particulate P (PP), particulate C (PC), particulate N (PN), suspended particulate organic matter (SPOM), nonvolatile suspended solids (NVSS), dissolved NO_3^-, dissolved NH_4^+, dissolved SRP, dissolved organic C (DOC), and suspended chlorophyll *a* (chl *a*). Sestonic molar ratios (C:N, C:P, N:P) were calculated from the PC, PN, and PP data.

We fixed samples for total and dissolved nutrient measurement with H_2SO_4 and froze them until analysis. We prepared and analyzed samples according to standard methods (Table 2). We did all spectrophotometry on a Varian Cary 50 UV-Vis spectrophotometer (Agilent Technologies, Santa Clara, California). We measured PC, PN, and sestonic C:N with a Thermo Flash EA1112 (Waltham, Massachusetts), DOC with a Shimadzu TOC-V_{CSH} (Colombia, Maryland), and chl *a* with a Turner Designs Trilogy fluorometer (Sunnyvale, California).

Data analyses

We averaged the values obtained from duplicate samples for each analyte from each site for each sampling event. We grouped all predictor variables into 2 groups, physiographic and LULC (Table S1). We defined physiographic variables as those that fit under the broad definition of physical geography, which includes climatology, geomorphology, and biogeography (Petersen et al. 2012). Longitude and mean annual rainfall at a site were strongly correlated ($r^2 = 0.92$, $p < 0.001$), so we used longitude as a proxy for rainfall. After grouping variables, we used principal components analysis (PCA) on continuous variables in each predictor data set to evaluate physiographic and LULC gradients and to assess patterns of covariation between predictors within each group. We had a large number of predictor variables, so we used patterns of covariation in the PCA for an initial round of data reduction by removing correlated variables (McCune and Grace 2002). We did not include ecoregion and season in the physiographic PCA to avoid an excessive variable-to-sample ratio (McCune and Grace 2002). We standardized data as *z*-scores, and ran all analyses on a correlation matrix.

We used redundancy analysis (RDA) to assess correlations among the remaining physiographic or LULC predictor variables and in-stream nutrient concentrations across the lower Brazos River watershed (Legendre and Legendre 2012). RDA assumes that predictor–response relationships are linear, so it is appropriate for environmental predictor–nutrient response data sets (ter Braak and Verdonschot 1995, Legendre and Legendre 2012). We conducted individual (physiographic vs LULC predictors), global (both predictor sets combined), and partial RDAs (both physiographic and LULC predictors, where the analysis is run on one set of predictors while controlling for the effect of the other) and used variance partitioning to evaluate the combined and pure effects of the 2 predictor sets (King et al. 2005, Peres-Neto et al. 2006, Legendre and Legendre 2012).

We used the first round of RDAs to further reduce our data. We identified and removed highly correlated predictors by back-sequential variance inflation factor (VIF) analysis, where the predictor with the largest VIF was removed and the analysis rerun until all VIF values were <10 (Dow et al. 2006). In the physiographic RDA, the standard deviations of slope at the reach and catchment scales were highly multicollinear with other variables (VIF = 47.7 and 34.0, respectively) and were removed. In the LULC RDA, % cultivated land at the catchment scale and % wetlands at the reach scale were highly multicollinear with other variables (VIF = 12886.8 and 136.1, respectively) and were removed. We ran permutation tests (minimum $n = 200$, $\alpha = 0.05$) to assess significance of individual, global, and partial effects models (Legendre and Legendre 2012). For all RDA models, we present the first 2 axes corrected by the R^2_{adj}, a more conservative measure of explanatory power than the "proportion of inertia explained" (Peres-Neto et al. 2006, Legendre and Legendre 2012).

Last, we used linear regression on annual average data to summarize univariate relationships between nutrients, physiographic, and LULC data. We averaged data for each nutrient for each site across sampling seasons. We used the predictor data sets from the final separate physiographic and LULC RDAs. The best-performing model for each nutrient was selected by applying the minimum Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2004). We used forward selection and assessed the categorical variable ecoregion with the whole-effect rule whereby it was added to the model only if all levels reduce the AICc. This approach resulted in 2 predictor models for each nutrient. In the RDA and linear-

Table 2. Nutrient data, abbreviation, units, analysis method, and references for our study. n/a = values were calculated. PC = particulate C, PP = particulate P, PN = particulate N.

Nutrient	Abbreviation	Units	Preparation	Method	Reference or method number
Total P	TP	μg/L	Whole water	Persulfate digestion, ascorbic acid-Mo blue	Wetzel and Likens 1991
Total N	TN	μg/L	Whole water	Persulfate digestion, 2nd-derivative spectrophotometry	Crumpton et al. 1992
Soluble reactive P	SRP	μg/L	Filtered water, GF/F	Ascorbic acid-Mo blue	Wetzel and Likens 1991
Particulate P	PP	μg/L	Residue, Pall A/E	Combustion and acid digestion, ascorbic acid-Mo blue	Wetzel and Likens 1991, Caston et al. 2009
NO_3^-		μg/L	Filtered water, GF/F	2nd-derivative spectrophotometry	Crumpton et al. 1992
NH_4^+		μg/L	Filtered water, GF/F	Phenate	Wetzel and Likens 1991
Particulate N	PN	mg/L	Residue, GF/F	Dynamic flash combustion	
Particulate C	PC	mg/L	Residue, GF/F	Dynamic flash combustion	
Dissolved organic C	DOC	mg/L	Filtered water, GF/F	Non-purgeable organic C	APHA 2005
Non-volatile suspended solids	NVSS	mg/L	Residue, Pall A/E	Mass loss after combustion at 500°C	US EPA Method 1684
Suspended particulate organic matter	SPOM	mg/L	Residue, Pall A/E	Mass loss after drying	US EPA Method 1684
C:N (seston)		molar	n/a	Calculated from PC and PN values	n/a
C:P (seston)		molar	n/a	Calculated from PC and PP values	n/a
N:P (seston)		molar	n/a	Calculated from PN and PP values	n/a
Chlorophyll *a*	chl *a*	μg/L	Residue, GF/F	Acetone extraction followed by fluorometry	Wetzel and Likens 1991
Temperature	Temp	°C	Field YSI Sonde		YSI Sonde Model 556 or Model 85
Dissolved O_2	DO	mg/L	Field YSI Sonde		YSI Sonde Model 556 or Model 85
pH			Field YSI Sonde		YSI Sonde Model 556 or Model 85

regression analyses, we $\log_{10}(x)$-transformed nutrient concentrations to meet the assumption of normality. We ran all univariate statistics in JMP 9.0 (SAS Institute, Cary, North Carolina). We did multivariate ordination (PCA and RDA) and variance partitioning with the *vegan* package (Oksanen et al. 2012) in R (version 2.0-5; R Project for Statistical Computing, Vienna, Austria).

RESULTS

Physiographic gradients and regional LULC patterns

The physiographic-variable PCA accounted for 73.7% of the variation among sites on the first 2 axes (Fig. 2A, B). Principal component axis 1 (PCA1) explained 58.8% of the variation among sites. All measures of slope (mean, maximum, and standard deviation [SD]) at all scales (reach, riparian, and catchment) had qualitatively similar influence along this axis. In general, PCA1 represented a gradient from sites with greater stream density and longitude (negative loadings on PCA1) to sites with greater mean, maximum, and SD of slope (positive loadings on PCA1). Sites were ordered on PCA1 along an east-to-west gradient in the Brazos watershed. PCA2 also represented a geographic gradient of more southern and western sites in the watershed (i.e., lower latitude and greater longitude) combined with a geomorphic gradient of higher stream density and larger catchment areas in the southern portions of the watershed (negative loadings along PCA2) to more north-

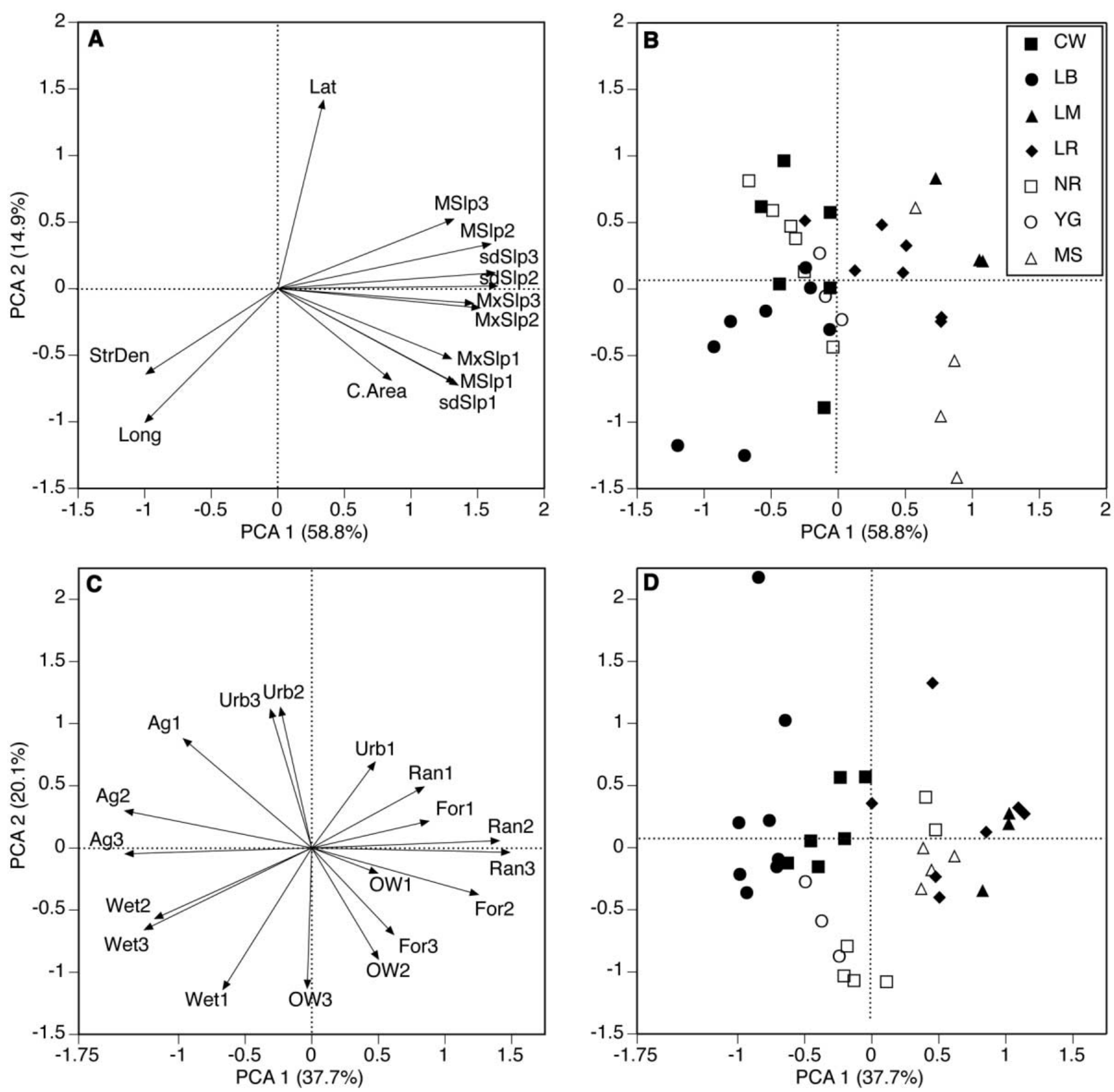

Figure 2. Principal component analysis (PCA) of continuous variables used in our study. A.—Multivariate relationships among physiographic variables. B.—Ordination of sampling sites in the physiographic PCA. C.—Multivariate relationships among land use/land cover (LULC) variables. D.—Ordination of the sampling sites in the LULC PCA. See Table 1 for abbreviations.

ern sites (i.e., greater latitude, positive loadings on PCA2). Thus, the physiographic PCA detailed the geographic position of sites within the watershed, and the combined gradients represented watershed-scale variation of southeastern, higher rainfall, and lower-slope sites to northwestern, steeper-slope sites with lower rainfall.

The LULC PCA also described a large-scale geographic gradient in LULC patterns throughout the watershed (Fig. 2C, D). The first 2 axes explained 57.8% of the variation among sites. PCA1 accounted for 37.7% of the variation among sites and described a gradient of sites characterized by catchment- and riparian-scale % cultivated land or a greater % wetland (negative loadings on PCA1) to a greater proportion of catchment- and riparian-scale % rangeland and % forest (positive loadings on PCA1). In general, this axis described watershed-scale patterns along a southeastern to northwestern gradient and a landuse-intensity gradient. Sites in the lower portion of the watershed were characterized by cultivated land and wetlands, and sites in the upper portion of the watershed were characterized by forest and rangeland. PCA2 represented a gradient of sites with higher catchment-scale % open water and reach-scale % wetland (negative loadings on PCA2) to sites with higher catchment- and riparian-scale % urban use and reach-scale % cultivated land (positive loadings on PCA2). This axis also showed variation in site-level LULC within subwatersheds. For example, sites in the lower Brazos tributaries (LB sites in Fig. 2D) typically have lower % rangeland and % forest and higher % cultivated land (i.e., consistent positions along PCA1), but individual sites within this section of the Brazos varied greatly in their % urban use vs % wetland (i.e., variable positions along PCA2). For all subwatersheds, variability along PCA2 was greater than the variability along PCA1, highlighting the difference between regional and reach LULC gradients.

The PCAs clearly showed that riparian-scale predictors were highly correlated with catchment-scale predictors, and the eigenvectors were of similar length for nearly all multiscale physiographic and LULC predictors (e.g., slope mean, maximum, and SD, and percentages of different LULC types; Fig. 2A, C). Percent forest and % open water were correlated at the riparian and catchment scales, but the strength of these relationships was not as great as the strength of the relationships among the other predictor variables. Overall, these results indicated that the riparian- and catchment-scale variables had similar information and explanatory power. Thus, we elected to run all subsequent models without riparian-scale predictors.

Nutrient responses to physiographic and LULC gradients

The first 2 physiographic RDA axes accounted for 27.1% of the variation in nutrient concentrations (R^2_{adj} = 0.39, $p <$ 0.005; Fig. 3A). The 1st RDA axis (RDA1) explained 17.8% of the variation in nutrients and represented a southeast–northwest gradient in the watershed. Southeastern sites in the WGCP ecoregion were characterized by higher concentrations of total and dissolved nutrients (TP, TN, SRP, NO_3^-, NH_4^+), which were positively correlated with stream density and site longitude. In contrast, northwestern sites in the EDPL ecoregion were characterized by greater reach-scale maximum slope and reach- and catchment-scale mean slope, which were negatively correlated with total and dissolved nutrients and positively correlated with higher seston C:P and N:P (indicating lower P content of seston). The 2nd physiographic RDA axis (RDA2) was strongly influenced by catchment-scale maximum slope and catchment area. Particulate matter and suspended algal biomass and higher seston C:N were positively correlated with catchment area and spring sampling period. The physiographic RDA indicated that ECTP and TBPR ecoregions and summer sampling season were weak predictors of nutrients.

The first 2 LULC RDA axes accounted for 20.6% of the variation in the data (R^2_{adj} = 0.26, p < 0.005; Fig. 3B). The RDA1 explained 13.4% of the variation in nutrients and represented a gradient of increased % forest and rangeland (at reach and catchment scales) to sites with higher catchment-scale % urban use and reach-scale % cultivated land. Percent forest and % rangeland were correlated with low total and dissolved nutrients and higher seston C:P and N:P, whereas % urban use and % cultivated land were correlated with total and dissolved nutrients. Much like the physiographic RDA, the LULC RDA1 axis represented a northwestern–southeastern spatial gradient across the Brazos watershed. RDA2 was a gradient of sites with greater % open water (especially at the reach-scale) to sites with higher reach-scale % urban use. Along this axis, greater % open water was correlated with higher particulate concentrations (PC, PN, SPOM, and NVSS) and suspended chl *a*, whereas watershed-scale % urban use catchment was positively correlated with greater dissolved nutient concentrations (especially NH_4^+ and SRP) and lower concentrations of suspended matter. DO, pH, DOC, and water temperature had relatively weak responses to LULC variables.

In the combined physiographic and LULC RDA, the first 2 axes accounted for 33.0% of the variation (R^2_{adj} = 0.51, p < 0.005; Fig. 3C) for the model. RDA1 explained 20.2% of the variation in nutrients. Physiographic and LULC predictors were strongly correlated across the watershed (Fig. 3C). Sites with higher stream density were associated with higher reach-scale % cultivated land and catchment-scale % urban use; these predictors were positively correlated with nutrient concentrations (both total and dissolved fractions) and these sites more commonly occurred in the WGCP ecoregion. Reach-scale % urban use was correlated with elevated DO, pH, and DOC, and these variables were higher in the winter (Fig. 3C). Percent forest (at both scales) and catchment-scale % rangeland were correlated with steeper and more variable slopes

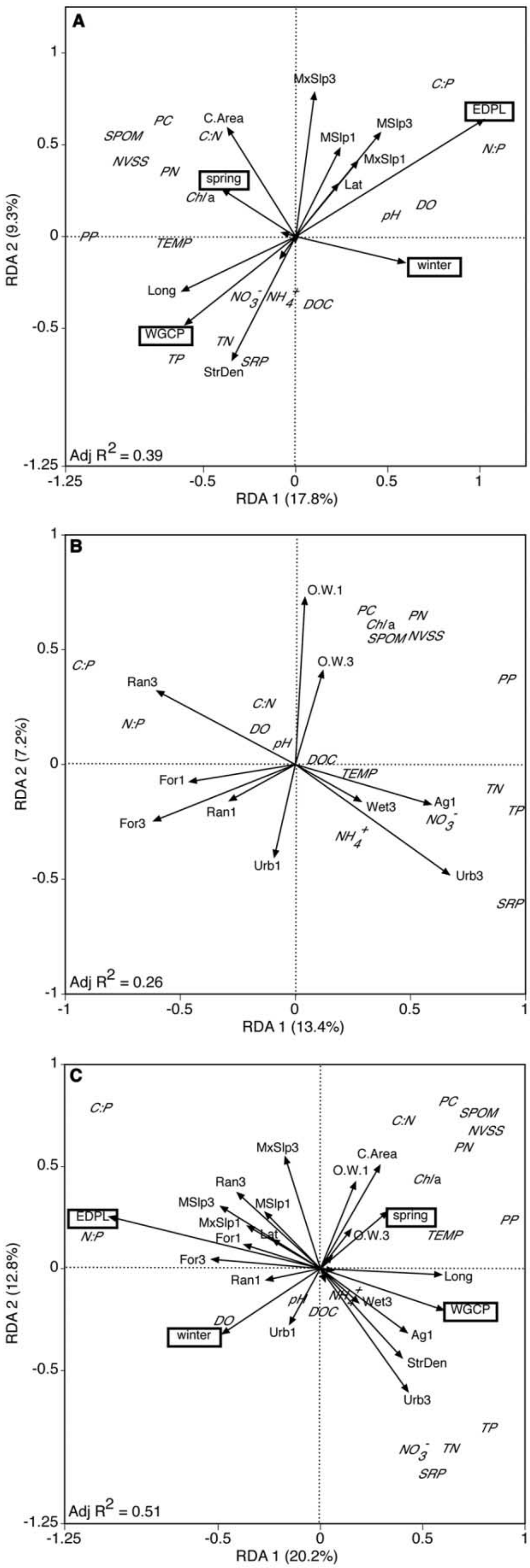

Figure 3. Redundancy Analysis (RDA) plots of the relationships between predictor groups and nutrient concentrations in the Brazos River. A.—Relationships among nutrient variables (italics) and physiographic variables. ECTP, TBPR, and summer sampling season are not shown because they plotted near the origin. B.—Relationships among nutrient variables and land use/land cover (LULC) predictors. C.—Global analysis including both groups of predictors. Boxes highlight categorical predictor variables. ECTP, TBPR, and summer sampling season are not shown because they plotted near the origin. See Tables 1 and 2 for abbreviations.

(at both scales). These sites predominantly occurred in the EDPL ecoregion and had higher seston C:P and N:P. Catchment area was positively correlated with % open water at both scales, and suspended particulate materials, suspended chl *a*, and seston C:N were higher in these larger watersheds, notably during the spring sampling season (Fig. 3C).

Partial effects and variance partitioning of physiographic and LULC data

The RDA used to assess the pure effects of physiographic variables explained 16.4% of the variation in the nutrient and water-quality data within the first 2 axes (R^2_{adj} = 0.25, p < 0.005; Fig. 4A) for the model. Total nutrients, SRP, and NO_3^- were positively correlated with latitude and were generally higher in the TBPR ecoregion, but were negatively correlated with stream density. NH_4^+ and seston C:P were positively correlated with stream density and were generally higher in the summer and in the EDPL and WGCP ecoregions. Catchment area was positively correlated with suspended particulate material, and nutrient concentrations were elevated in spring. Seston N:P and DOC were positively correlated with winter samples, but were negatively correlated with catchment area and spring samples. This analysis also indicated that maximum and mean slopes and longitude were relatively weak predictors of nutrient concentrations.

The RDA used to assess the pure effects of LULC predictors explained 8.8% of the variation in the nutrient and water-quality data within the first 2 axes (R^2_{adj} = 0.12; p < 0.005; Fig. 4B). TN and NO_3^- responded strongly and positively to catchment-scale % urban use. Total P and SRP were positively influenced by catchment-scale % urban use and by reach-scale % rangeland. Suspended particulate matter and NH_4^+ were correlated with reach-scale % rangeland, whereas suspended chl *a*, DOC, and seston C:N were most strongly correlated with reach-scale cultivated land. Seston C:P and N:P were positively associated with reach-scale % forest. Reach-scale % open water and catchment-scale % rangeland had weak influence on nutrient concentrations and water-quality conditions.

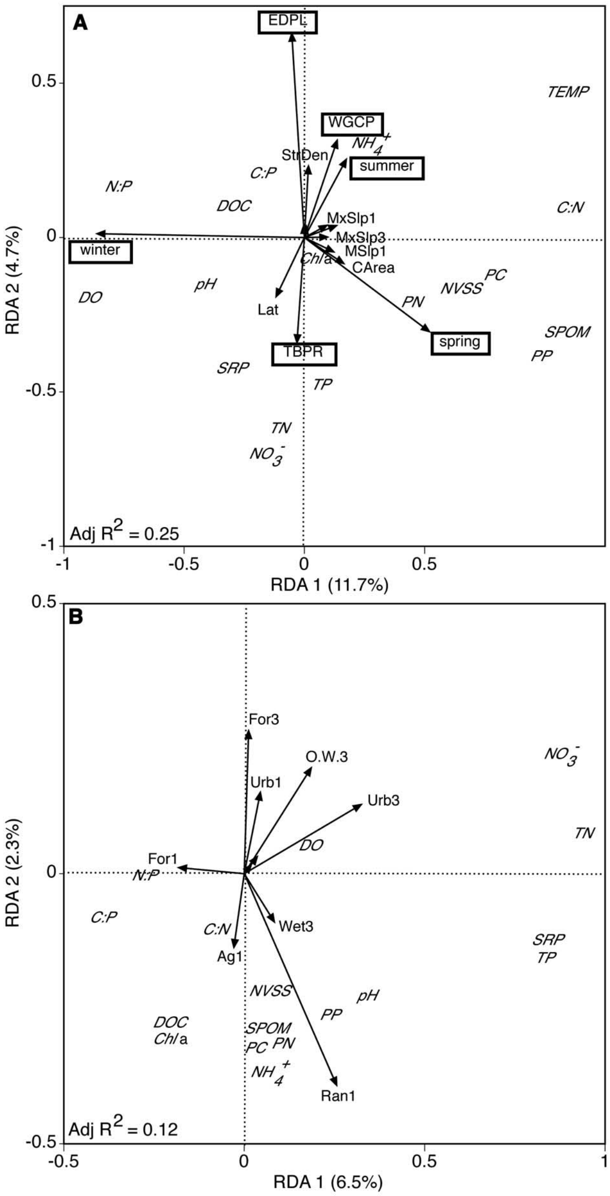

Figure 4. Partial Redundancy Analysis (RDA) plots of relationships between predictor groups and nutrient concentrations in the Brazos River. A.—Relationships among nutrient variables (italics) and physiographic predictors after accounting for the influence of land use/land cover (LULC) predictors. ECTP ecoregion, Long, and MSlp3 are not shown because they plotted near the origin. B.—Relationships among nutrient variables and LULC predictors after accounting for the influence of physiographic predictors. Wat1, Ran3, and *TEMP* are not indicated because they plotted near the origin. See Tables 1 and 2 for abbreviations.

Physiographic and LULC RDAs explained significant amounts of the variation in nutrient and water-quality data, but variance partitioning indicated that physiographic variables accounted for 25.1% of the variation, ~2× the independent explanatory power of LULC variables (11.6%). The 2 data sets overlapped substantially (13.9%), a result that indicated the extent of collinearity among predictors. Much of this collinearity could be attributed to 3 groups of predictors (Fig. 3C): 1) reach-scale mean and maximum slope and catchment-scale mean slope were highly correlated with % forest at both scales and catchment-scale % rangeland; 2) catchment area and open water (at both scales) were highly correlated; and 3) stream density was highly correlated with reach-scale % cultivated land and catchment-scale % urban use. Both physiographic and LULC variables provided substantial independent explanatory power and combined to explain >½ of the variation in nutrient conditions throughout the Brazos watershed.

The sets of predictors identified by the regressions were similar to those identified by the multivariate analyses (Table 3), especially for predictors that were strongly correlated with the 1st axes of the RDAs. We found significant models for all nutrients except the NO_3^-–physiographic combination. Regressions identified some negative correlations between predictors and nutrient responses that might be missed by visual inspection of RDA plots, but the similarity of results and ease of graphical interpretation led us to focus our discussion on the multivariate results.

DISCUSSION

Our primary goal was to assess the degree to which relatively static measures of physiographic environmental conditions and patterns of LULC could predict nutrient conditions in a large riverine system. Contrary to our 1st hypothesis, variance partitioning indicated that at the whole-watershed level, baseline water chemistry was more strongly affected by physiographic environmental gradients than by LULC patterns. However, in agreement with our 2nd hypothesis, the effects of physiographic environmental gradients and patterns of LULC depended on the response variable and category of predictor, and effects differed between reach and catchment scales. The effect of LULC on nutrient concentrations was difficult to separate from the effect of physiographic environmental gradients even though the substantial effect of LULC on nutrient concentrations indicated an intensity-of-human-modification gradient.

Physiographic gradients and regional LULC patterns in the Brazos River watershed

We observed large-scale spatial variation in both physiographic and LULC characteristics across the Brazos watershed. Physiographic and LULC gradients covaried, and ordinations of both sets of data approximated the northwest-to-southeast spatial arrangement of sites. Addition of physiographic data to our analysis revealed that LULC patterns are strongly influenced by existing natural gradients in the watershed. The northwestern portions of the watershed, primarily in the Lampasas and upper Little River sub-

Table 3. Results of multiple regression analyses testing the ability of physiographic and land use/land cover (LULC) variables to predict in-stream nutrient concentrations. The models with the lowest Akaike Information Criterion for small samples (AICc) score are listed. CR = coefficient of regression for the selected predictors. Coefficients for ecoregion are not given because each ecoregion could have individual values, and it was included as a whole effect only. Bold indicates $p < 0.05$. See Table 1 for abbreviations.

Nutrient response	Best model	R^2adj	CR	p
Physiographic models				
TP	Long (+), StrDen (+)	0.32	0.81, 2.0	**<0.001**
TN	MSlp3 (–)	0.10	–0.63	**0.033**
SRP	StrDen (+), MxSlp3 (–)	0.25	1.79, –0.04	**0.003**
PP	Lat (+), Long (+), C.Area (+), StrDen (+)	0.60	0.62, 0.66, 0.00002, 1.68	**<0.001**
NO_3^-	StrDen (+)	0.05	1.62	0.110
NH_4^+	StrDen (+)	0.19	0.78	**0.004**
PN	Lat (+), Long (+), C.Area (+), MxSlp1 (–)	0.50	0.55, 0.62, 0.00001, –0.001	**<0.001**
PC	Lat (+), Long (+), C.Area (+)	0.49	0.50, 0.41, 0.00002	**<0.001**
DOC	MxSlp1 (–)	0.23	–0.033	**0.002**
NVSS	Lat (+), Long (+), C.Area (+)	0.48	1.38, 1.87, 0.00002	**<0.001**
SPOM	Lat (+), Long (+), C.Area (+)	0.49	0.64, 0.71, 0.00002	**<0.001**
C:N	Lat (+), C.Area(+), MSlp1 (+), MSlp3 (+), Ecoregion	0.56	0.15, 0.000004, 0.04, 0.20	**<0.001**
C:P	Long (–), StrDen (–), MSlp1 (+), MSlp3 (+)	0.69	–0.19, –1.04, 0.09, 0.21	**<0.001**
N:P	StrDen (–), MxSlp1 (+), MSlp3 (+)	0.60	–0.95, 0.02, 0.32	**<0.001**
Chl *a*	Lat (+), C.Area (+), MxSlp1 (–), Ecoregion	0.46	0.76, 0.00002, –0.002	**<0.001**
Temp	Lat (–), Long (+)	0.58	–1.65, 1.85	**<0.001**
DO	Long (–), C.Area (+)	0.26	–1.83, 0.00002	**0.002**
pH	Long (–)	0.16	–0.2	**0.014**
LULC models				
TP	Urb1 (–), Urb3 (+), For3 (–), Wet3 (+)	0.64	–0.08, 0.10, –0.048, 0.12	**<0.001**
TN	Urb1 (–), Urb3 (+)	0.40	–0.05, 0.08	**<0.001**
SRP	Urb1 (–), Urb3 (+)	0.44	–0.13, 0.14	**<0.001**
PP	Ag1 (+), O.W.1 (+), For3 (–), O.W.3 (+)	0.48	0.02, 0.02, –0.03, 0.50	**<0.001**
NO_3^-	Urb3 (+)	0.35	0.09	**<0.001**
NH_4^+	Urb3 (+), O.W.3 (–)	0.16	0.01, –0.18	**0.019**
PN	Ag1 (+), O.W.1 (+), For3 (–), O.W.3 (+)	0.44	0.01, 0.02, –0.02, 0.51	**<0.001**
PC	O.W.1 (+), For3 (–), O.W.3 (+)	0.44	0.03, –0.03, 0.34	**<0.001**
DOC	Ran1 (+), Urb3 (–), Ran3 (–)	0.20	0.01, –0.01, –0.01	**0.016**
NVSS	Urb1 (–), For3 (–), O.W.3 (+)	0.52	–0.08, –0.10, 1.25	**<0.001**
SPOM	Urb1 (–), O.W.1 (+), For3 (–), O.W.3 (+)	0.45	–0.03, 0.02, –0.04, 0.47	**<0.001**
C:N	Ran3 (+), For3 (–)	0.48	0.01, –0.01	**<0.001**
C:P	Urb1 (+), For1 (–), Urb3 (–), Ran3 (+)	0.76	0.03, –0.006, –0.04, 0.02	**<0.001**
N:P	Urb1 (+), Urb3 (–), Ran3 (+), For3 (+)	0.69	0.03, –0.03, 0.01, 0.02	**<0.001**
Chl *a*	O.W.1 (+), For3 (–), O.W.3 (+)	0.38	0.02, –0.05, 0.62	**<0.001**
Temp	O.W.1 (+), Ran3 (–)	0.40	0.05, –0.08	**<0.001**
DO	Ran3 (+)	0.25	0.05	**0.001**
pH	Ran1 (+), O.W.1(+)	0.28	0.01, 0.007	**0.001**

watersheds are more arid, have more variable topography, and have geology and soils typical of the EDPL ecoregion, which is characterized by shallow limestone bedrock with little topsoil development (Barnes 1992, NRCS 2008, USEPA 2012). Consequently, many of the LULC patterns in EDPL ecoregion of the Brazos watershed are typical of more low-intensity human activities, and % forest and % rangeland is higher than elsewhere in the watershed. In contrast, the gentler topography and higher annual precipitation of the southeastern portion of the watershed in the WGCP ecoregion were correlated with higher stream density and deep, clay soils (Barnes 1992, NRCS 2008, USEPA 2012). Higher precipitation and greater floodplain connectivity were associated with higher % cultivated land and % urban use. Both physiographic and LULC predictors described a substantial portion of the variation among sites, but physiographic predictors explained substantially more LULC predictors (73.7 vs 58.8%). Thus, physiographic context can strongly influence spatial patterns of LULC, a result highlighting the importance of considering both groups of data, especially in large riverscapes (Allan 2004, King et al. 2005).

Nutrient responses to physiographic gradients

Watershed-scale patterns in physiographic gradients strongly influenced spatial patterns of in-stream nutrient concentrations in the Brazos River. In-stream nutrients tended to be dominated by dissolved forms, which accounted for 71 and 94% of the total N and P, respectively (Table S3). Higher concentrations of total and dissolved nutrients were positively correlated with longitude (and thus, mean annual rainfall) and stream density. These sites were largely situated in the WGCP ecoregion. In-stream TN, NO_3^-, and NH_4^+ concentrations were positively correlated with stream density and negatively correlated with slope, conditions that increase the land–water contact and decrease flow velocity and, thus, increase opportunity for higher N inputs from agriculture (Dodds and Oakes 2006, Howarth et al. 2012). In-stream P (all forms) was higher in the eastern portions of the watershed where mean annual rainfall was higher. In the eastern WGCP ecoregion, deep, clay soils dominate (Barnes 1992, USEPA 2012), and erosional processes deliver relatively high P sediments to the river (Calhoun et al. 2002, Banner et al. 2009). In contrast, groundwater in the northwestern EDPL ecoregion is often low in P and has elevated CO_3^{2-} concentrations (Groeger and Gustafson 1994). Last, seston C:P and N:P were higher in the more-arid EDPL ecoregion, indicating low in-stream P availability in this ecoregion.

Particulate matter (particulate C, N, P, SPOM, NVSS, and suspended chl *a*) was strongly correlated with catchment area and spring sampling. All of these responses generally increased along the west-to-east rainfall gradient in the watershed. This pattern is consistent with the greater potential for runoff and transport of fine particles and sediment to downstream reaches in larger subwatersheds (Dodds and Whiles 2004, Bernot and Dodds 2005). Chl *a* also was elevated in these areas because primary production is often higher in open-canopy areas of large rivers than in closed-canopy smaller rivers (Grimm et al. 2005). Higher discharge in the downstream and eastern portions of the Brazos watershed, especially during the relatively wet spring season, would enhance this pattern (Sharpley et al. 2008, Banner et al. 2009). C:N of suspended particulate material was positively correlated with catchment area, a pattern that is consistent with increasing inputs of allochthonous and refractory C material with low N content from the watershed (Wildhaber et al. 2012).

Nutrient responses to LULC gradients

Reach-scale % cultivated land was significantly associated with increased in-stream TN, NO_3^-, and TP concentrations, consistent with results of other studies (Dodds and Oakes 2006, 2008, Arango and Tank 2008, Banner et al. 2009). NO_3^- is typically highly mobile in soils, thus NO_3^- applied as fertilizer enters aquatic systems in dissolved and labile form (Haggard et al. 2003). NH_4^+ was correlated with both reach- and catchment-scale % urban use. Sliva and Williams (2001) also found a correlation between NH_4^+ and both reach- and catchment-scale % urban use during spring and summer. The correlation between NH_4^+ and % urban use is often attributed to wastewater treatment plants, leaky sewer and septic systems, and runoff of materials derived from automobile traffic (Paul and Meyer 2001, Hope et al. 2004, Bernhardt et al. 2008).

We were unable to directly assess differences in effects of % cultivated land between scales because of multicollinearity, but the high degree of correlation between scales suggests that the effect of % cultivated land is not scale dependent. However, the effect of % urban use appears to differ substantially between scales. Reach-scale % urban use was negatively correlated with suspended particulate matter, and catchment-scale % urban use was positively correlated with total and dissolved nutrients. Most investigators assume that urban land use leads to increased particulate inputs to streams, but Dodds and Whiles (2004) suggested that urban land use may reduce sediment loading to streams by reducing the amount of exposed erodible soil and that the effects of urban LULC on sediment loading may attenuate quickly downstream. This reasoning could explain the negative correlation between reach-scale % urban use and PP (and the other particulate variables). Moreover, reach- and catchment-scale effects may not be mutually exclusive. TP and reach-scale % cultivated land were correlated as were SRP and catchment-scale % urban use. Other investigators have found a positive correlation between % urban use and SRP in small-to-medium-sized watersheds (Brett et al. 2005, Sonoda and Yeakley 2007). Reach-scale % urban use may have a quickly attenuated effect on PP that is independent of, or overridden by, the regional effect of catchment-scale % urban use on SRP, the dominant fraction of P in these systems. Seston C:P and N:P were positively correlated with catchment-scale % rangeland. Grasses (the dominant plant in rangeland) retain more P in the watershed than forest. The net result would be elevation of both ratios (Osborne and Kovacic 1993, Sliva and Williams 2001). Seston C:P also might respond negatively to reach-scale % cultivated land (James et al. 2007). The correlation of C:P and N:P with catchment-scale % rangeland suggests that rangelands may retain P more efficiently than forest. Allochthonous inputs are likely to be relatively high in C, whereas N delivery is likely to occur via groundwater and nutrient recycling pathways (Haggard et al. 2003, Bernot and Dodds 2005, Arango and Tank 2008).

Partitioning the effects of physiographic and LULC gradients

Few researchers have tried to untangle individual and combined effects of physiographic (or geologic) variables and LULC predictors on river nutrient conditions (but see Dow et al. 2006) even though LULC and physiographic conditions frequently are coupled (Allan 2004, King et al. 2005). In our study, the primary covariation was related to regional spatial variation in physiography and LULC patterns in 2 of the more prominent ecoregions in the watershed (EDPL and WGCP). The gradient of physiographic conditions (stream density and eastern locations to steeper slopes and western locations) was aligned with an LULC intensity gradient. This result highlights the issues of covariation between physiographic and LULC features (Allan 2004, King et al. 2005) and indicates that further investigation into the degree of covariation is needed.

Variance partitioning revealed new aspects of physiographic influences on nutrient conditions. In the absence of LULC effects, the influence of season (especially spring and winter) on in-stream nutrients was much stronger. Catchment area and spring sampling were correlated with elevated particulate material and nutrients, and reach-scale mean slope was associated with higher in-stream particulate nutrients. These patterns are consistent with the correlation between total suspended solids and slope variability found by Sliva and Williams (2001). When we controlled for LULC, the effects of ecoregion, latitude, and stream density became secondary. The TBPR ecoregion was associated with elevated TN, NO_3^-, TP, and SRP in the conditioned analysis but not in the unconditioned analysis. However, the WGCP ecoregion and summer sampling remained associated with elevated NH_4^+ concentrations in the conditioned analysis. Elevated NH_4^+ could result from agriculture or decomposition of organic matter during low-flow periods when in-stream N recycling, also likely to be higher in the summer, is elevated (Sliva and Williams 2001, Dodds and Oakes 2008).

Variance partitioning also revealed new aspects of LULC influences on nutrient conditions. In the absence of physiographic effects, the importance of catchment-scale % rangeland and reach-scale % open water were minimized, but the LULC intensity gradient between catchment-scale % urban use and reach-scale % forest remained important. The minimal influence of catchment-scale rangeland and reach-scale % open water in the partial RDA suggests that their explanatory value was related primarily to physiography. In the partial RDA, catchment-scale % urban use was most closely associated with higher TN and NO_3^- concentrations, consistent with the expected effect of % urban use on nutrients (Paul and Meyer 2001). Particulate nutrients and seston C:N were positively associated with reach-scale % cultivated land and reach-scale % rangeland and negatively correlated with catchment-scale % forest. This pattern differed substantially from the pattern in the global analysis in which particulate matter and seston C:N were positively correlated with % open water, but it is consistent with the idea that forests retain organic matter and suspended solids on the landscape (Kaplan et al. 2006). The lack of an association between these variables and reach-scale % forest suggests that the processes by which nutrients are retained on the landscape operate at broad scales and that catchment-level processes can override the ability of reach-scale processes to retain nutrients on the landscape (Arango and Tank 2008, Filoso and Palmer 2011).

Many investigators have found that watershed conditions and land use affect aquatic nutrient dynamics (reviewed by Allan 2004, Johnson and Host 2010). However, we did not expect to find that 51% of the variability in nutrients could be explained by variables that probably change on decadal or greater time scales and that physiographic predictors accounted for 2× as much of the total explained variation as LULC predictors (25 vs 12%, respectively). Nevertheless, our analysis suggests that both physiographic and LULC data sets are needed to understand the independent effects of both factors. To our knowledge, the only other investigators to use similar variance-partitioning techniques are Dow et al. (2006). Like us, they found substantial overlap between LULC and geological predictors, but in contrast to us, they found that LULC explained more of the variation in aquatic ion concentrations than geology did. Dow et al. (2006) sampled a smaller geographic area more intensively than we did, which may partially account for the higher proportion of variance explained in their study (75 and 87% in the 2 watersheds they assessed) and the greater influence of LULC predictors, which may exert stronger effects at smaller spatial scales (Goldstein et al. 2007).

Conclusion

Physiographic conditions appear to set the context within which nutrients are controlled in large lotic systems. LULC is highly correlated with physiography but has significant independent effects on nutrient concentrations. This information is important for designing management or restoration projects. Application of appropriate restoration measures and realistic expectations of the benefits of a given project require a fundamental understanding that a stream reach is part of a larger landscape. Including physiographic predictors in riverscape studies probably will be most beneficial in large systems that span large areas, where environmental gradients can have stronger influences than LULC (Goldstein et al. 2007), or in smaller systems that have particularly steep environmental gradients (Malmqvist 2002). Our results highlight the influence of largely static physiographic conditions and long-term patterns of climate and LULC on aquatic systems.

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