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Climate Mediates Land-use and Within-lake Drivers of Seston Stoichiometry: A Large-scale Assessment Across Tropical Shallow Lakes

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Abstract

Seston stoichiometry links nutrient availability to the structure and functioning of aquatic food webs, yet how in-lake conditions interact with broader climatic, geomorphological and land-use drivers to shape seston carbon-to-phosphorus (C:P) ratios remains poorly understood in tropical systems. We used regression tree analysis (RTA) to evaluate the relative importance of in-lake, lake-catchment and climate variables in explaining seston C:P ratio variation across 95 shallow lakes and reservoirs spanning a semi-arid-to-humid climatic gradient in northeastern Brazil. The RTA explained nearly half of the variance in seston C:P ratio (49.6%) and revealed a hierarchical structure among predictors. Cumulative precipitation over the two years preceding sampling was the primary split, separating lakes below and above 882 mm. Among wetter lakes, total dissolved phosphorus (TDP) was the only additional predictor, and the highest C:P ratios occurred where TDP was also high, suggesting that hydrological inputs deliver carbon-rich particulate material alongside dissolved phosphorus rather than alleviating phosphorus limitation. Among drier lakes, the partial pressure of CO_2 (pCO_2) was the dominant secondary predictor, with high pCO_2 associated with elevated seston C:P ratio, while land use, reflecting the proportion of anthropogenic catchment area, further refined predictions, with more anthropized catchments showing higher seston C:P ratios. These results show that precipitation establishes a hydrological template within which phosphorus availability, inorganic carbon supply and land use jointly shape seston stoichiometry, reinforcing the importance of integrating climatic, landscape and in-lake variables to predict nutrient cycling in tropical freshwater ecosystems under climate and land-use change.

INTRODUCTION

Lakes play a central role in supporting human societies by providing water resources, fisheries and other ecosystem services (Daily et al. 1997; Esteves et al. 2008; Schallenberg et al. 2013; Vasishtha and Ganguly 2020). Their importance is particularly pronounced in water-scarce regions such as arid and semi-arid environments, where freshwater systems represent critical ecological and socio-economic resources and where drylands are projected to expand under climate change (Cirilo et al. 2017; Huang et al. 2016). Many of the ecological processes underlying these services are regulated by planktonic communities, which consist of microscopic organisms suspended in the water column (Janssen et al. 2021; Naselli-Flores and Padisák 2023). Within these communities, phytoplankton play a central role as primary producers that sustain aquatic food webs and influence ecosystem functioning (Havens, 1998; Korhonen et al. 2011; Mao et al. 2020; Costa et al. 2024). Together with heterotrophic microorganisms and inorganic particles, phytoplankton form seston, the pool of suspended particles in the water column whose elemental composition integrates biological production and environmental inputs (Hutchinson 1967).

The elemental composition of planktonic biomass has long been described using the Redfield ratio of carbon (C), nitrogen (N) and phosphorus (P) (106:16:1), originally derived from marine phytoplankton (Redfield 1934, 1958; Elser et al. 1996). Although seston includes several biotic and abiotic fractions, much of the theoretical framework linking elemental ratios to ecological processes has been developed primarily for phytoplankton, which often represents the dominant biological component of seston in lakes (Hessen 2006). Therefore, seston stoichiometry, such as carbon-to-phosphorus (C:P) ratio, is widely used as an

indicator of nutrient limitation and ecosystem functioning in freshwater systems (Jiang and Nakano 2022). Because seston C:P ratio determines the nutritional quality of primary producers for higher trophic levels, shifts in seston C:P ratio can propagate through aquatic food webs and influence ecosystem functioning (Elser et al. 2000; Sterner and Elser, 2002; Karpowicz et al. 2021). However, accumulating evidence shows that phytoplankton stoichiometry can vary substantially depending on environmental conditions and species composition and physiological strategies (Litchman and Klausmeier, 2008; Yvon-Durocher et al. 2017; Heinrichs et al. 2024). For example, high temperatures may increase cellular C:P and N:P ratios due to greater enzymatic efficiency and reduced investment in phosphorus-rich molecules such as ribosomal RNA and phospholipids (Geider and La Roche 2002). Similarly, changes in nutrient supply or light availability can alter phytoplankton growth and nutrient storage dynamics, leading to shifts in seston stoichiometry as predicted by the light-nutrient hypothesis (Dickman et al. 2006; Sterner et al. 1997).

Environmental drivers capable of altering seston stoichiometry operate across multiple spatial scales (Chiandet and Xenopoulos 2011). At the scale of individual lakes, in-lake physicochemical conditions such as nutrient availability, light penetration and dissolved inorganic carbon concentrations directly influence phytoplankton growth and elemental composition. These factors can be considered proximate drivers of seston stoichiometry, as they act directly on phytoplankton species composition and physiology. In contrast, broader out-lake landscape and climatic characteristics, including catchment land use, lake morphometry and precipitation regimes, represent ultimate drivers that regulate the supply and concentration of nutrients, organic matter and energy entering aquatic ecosystems (Hessen 2006). Land use intensity, for instance, can determine the magnitude and stoichiometry of dissolved and particulate nutrient inputs from surrounding catchments (Carpenter et al. 1998; Vanni et al. 2011; Nobre et al. 2020; Wang et al. 2020). Precipitation can alter seston stoichiometry by modifying the runoff magnitude between catchments and lakes, and therefore, influencing both the delivery of nutrients and particulate material as well as the dilution capacity of aquatic ecosystems (Li et al. 2025; Liu et al. 2024; Nobre et al. 2020; Setubal et al. 2026). Finally, waterscape properties such as lake area, volume and morphometry, and landscape properties such as lake catchment size, slope and land cover can influence the entrance or retention of allochthonous material in lakes and, therefore, plankton dynamics, particularly in shallow lakes where interactions with surrounding landscapes are strong (Costa et al. 2024; Di Girolamo et al. 2025).

Despite growing knowledge about how individual drivers affect plankton stoichiometry, relatively few studies have investigated how proximate (in-lake) and ultimate (landscape and climatic) out-lake drivers interact to determine seston elemental composition at regional scales. Because out-lake drivers such as climate, land use and geomorphology integrate the broader landscape context that defines the lake-catchment waterscapes (Setubal et al. 2026), they may capture the cumulative effects of multiple environmental processes and potentially provide stronger predictive power of mechanisms affecting large-scale variation in seston stoichiometry than highly variable in-lake conditions. This possibility is particularly relevant to predict seston stoichiometry variation in lakes distributed along regions with strong climatic gradients and undergoing rapid land-use change. In this study, we investigated how seston C:P stoichiometry varies across 95 shallow tropical lakes distributed along a climatic gradient (semi-arid and humid) in northeastern Brazil. Specifically, we evaluated the relative importance of in-lake physicochemical and biological factors and out-lake climatic, geomorphological and land-use properties of the lake-catchment system in determining

variation in seston C:P stoichiometry. We hypothesize that broader landscape and climatic drivers may exert stronger control over seston stoichiometry than local lake variables because they integrate the watershed and environmental context shaping lake ecosystems.

MATERIALS AND METHODS

Study area

This study was conducted in the state of Rio Grande do Norte, northeastern Brazil, during the dry season of 2012 (Fig. 1). The dataset included 95 lentic systems (30 natural lakes and 65 reservoirs; hereafter lakes) distributed across 14 hydrographic basins and spanning a wide gradient of trophic status and catchment land-use intensity. The lakes studied are generally shallow (95% < 4-m deep), encompassing a wide gradient of trophic states ranging from oligotrophic to hypereutrophic conditions and showing a wide range of catchment land-use patterns, from relatively preserved landscapes to highly anthropized environments dominated by agriculture, pasture and urban areas (Cabral et al. 2019; Nobre et al. 2020). These ecosystems are distributed across two climatic domains according to the Köppen–Geiger classification: a semi-arid region (BSh climate), where annual precipitation ranges from approximately 400 to 800 mm, and a humid to sub-humid tropical coastal region where annual precipitation ranges from approximately 800 to 1200 mm (Silva et al. 2022).

Sampling design

Water samples were collected during the dry season (September 2012) to obtain a spatial snapshot of limnological conditions across the studied lakes. In each ecosystem, water samples were collected exclusively from the limnetic region to characterize pelagic conditions and minimize the direct influence of littoral vegetation and benthic and shoreline processes that could contribute to seston through resuspended sediments and fine particulate plant detritus.

Three sampling points were selected in the central region of each lake, and water subsamples (approximately 1 L) were collected from the subsurface layer of the water column (approximately 0.3 m depth) using a Van Dorn bottle. The three subsamples collected within each ecosystem were then integrated into a 10-L bucket as a single composite sample representing the average limnetic condition of each lake. This integrated sampling encompasses the limnetic spatial variability while preserving comparability among ecosystems distributed across broad spatial gradients (Soranno et al. 2017; Nobre et al. 2020).

Determination of seston C:P ratio and in-lake environmental predictors

Seston C:P stoichiometry was determined from suspended particulate matter collected from the water column. Depending on the amount of suspended particulate material, different aliquots of lake water (0.5 to 1.5 L) were filtered through pre-combusted and pre-weighed glass fiber filters (GF/F, 0.7 µm pore size). After filtration, filters were dried in an oven at 50°C until they reached constant weight and then weighed again. Seston dry mass retained on each filter was calculated as the difference between the filter weight before and

after filtration. The mass of seston together with the volume of water filtered through each filter was then used to standardize particulate carbon and particulate phosphorus concentrations per unit volume of water. Particulate carbon concentration was measured using a total carbon analyzer, whereas particulate phosphorus concentration was determined after persulfate digestion followed by colorimetric determination of soluble reactive phosphorus according to Murphy and Riley (1962). Carbon and phosphorus concentrations were then converted to molar units (mol L^{-1}), and the molar ratio between particulate carbon and phosphorus was calculated to obtain the seston C:P ratio used as the response variable in the analyses.

Several in-lake variables were measured as in-lake predictors of seston C:P. These endogenous variables included Secchi disc depth, chlorophyll-a concentration (Chl-a), total dissolved phosphorus (TDP), dissolved organic carbon (DOC), and partial pressure of carbon dioxide in water (pCO_2). Chl-a was determined following ethanol extraction and spectrophotometric measurement according to Jespersen and Christoffersen (1987) and was used as a proxy for phytoplankton biomass. High phytoplankton biomass can influence seston stoichiometry because phytoplankton populations typically present C:P ratios that substantially differ (lower) from inorganic sediment and fine suspended particulate organic detritus (Wetzel 2001).

TDP concentration was measured after persulfate oxidation following Valderrama (1981) and quantified using the colorimetric method of Murphy and Riley (1962). Phosphorus availability is one of the main drivers of phytoplankton growth and elemental composition, and increased phosphorus supply can reduce seston C:P ratios by alleviating nutrient limitation (Elser et al. 2003). DOC concentration was measured using a total carbon analyzer (TOC-V – Shimadzu). DOC may influence seston stoichiometry indirectly by reducing light penetration in the water column and by stimulating microbial pathways that can alter nutrient recycling and potentially support mixotrophic interactions (Costa et al. 2024). Before TDP and DOC analyses, lake water samples were filtered through pre-combusted GF/F filters (0.7 µm). The pCO_2 in water was used as a proxy for inorganic carbon availability to phytoplankton. It was estimated from measurements of pH and alkalinity using carbonate equilibrium equations with corrections for water temperature and wind velocity (Weiss 1974; Cole et al. 1994). Alkalinity was determined through acid neutralization capacity and pH was measured using a calibrated pH meter immediately after sampling to minimize CO_2 degassing artifacts. Variation in pCO_2 can influence phytoplankton carbon acquisition via photosynthesis and therefore may affect the carbon content of seston (Junger et al. 2019).

Determination of out-lake predictors: precipitation, geomorphological and land-use properties of the lake–catchment system

Precipitation data were obtained from meteorological stations operated by the Brazilian National Institute of Meteorology (INMET). Following the same procedure described by Nobre et al. (2020), precipitation magnitude was calculated as the cumulative monthly precipitation recorded along a two-year period before samplings, between September 2010 and September 2012 for each meteorological station. Seven INMET automatic weather stations distributed across the Rio Grande do Norte State were used to obtain precipitation data.

To estimate precipitation values for each lake, a spatial interpolation procedure was applied in which the precipitation values from the meteorological stations were combined using a weighted average, with weights proportional to the inverse of the distance between each station and each lake. This approach allows capturing spatial variability in precipitation across the study region and has been shown to produce precipitation estimates consistent with regional climatological patterns (Fick and Hijmans 2017; Nobre et al. 2020).

External predictors describing the geomorphological and land-use characteristics of the lake–catchment system included lake perimeter (LP), lake area (LA), the ratio between perimeter and area (LP:LA), shoreline development (SD), catchment area (CA), the ratio between lake area and catchment area (LA:CA), and mean catchment slope (MCS). These variables describe the physical structure of lake–catchment systems and can influence the magnitude of terrestrial inputs reaching aquatic ecosystems.

Lake perimeter, lake area and shoreline development were obtained from satellite images through polygon delineation using ArcGIS 10.5.1 (ESRI 2017). Maximum depth of each lake was measured in the field using a calibrated rope. Catchment boundaries were delineated using the ArcHydro toolbox in ArcGIS based on digital elevation models obtained from the Brazilian Geomorphometric Database (TOPODATA). Mean catchment slope (MCS) was calculated using the slope function applied to a 30-m digital elevation model.

Land-use properties within catchments were quantified using spatial land-cover data from the MapBiomas Project (Collection 3). Anthropogenic land use included cropland, pasture and urban/developed areas. For each catchment, four variables were calculated: catchment anthropogenic area (CAA), the percentage of anthropogenic area relative to catchment area (CARel), the ratio between anthropogenic catchment area and lake area (CAA:LA), and the ratio between anthropogenic catchment area and lake perimeter (CAA:LP). These variables represent the magnitude and spatial distribution of human land use in the catchment and are expected to influence nutrient and sediment inputs to lakes (Foley et al. 2005; Vanni et al. 2011; Nobre et al. 2020).

Data analysis

To evaluate how seston C:P ratios responded to environmental drivers operating at multiple spatial scales, we applied Regression Tree Analysis (RTA) following the framework described by Breiman et al. (1984) and De'ath and Fabricius (2000). RTA is a non-parametric statistical technique that partitions the variation of a response variable by recursively splitting the dataset according to explanatory variables. This approach is particularly suitable for ecological datasets because it can detect nonlinear relationships, hierarchical effects and interactions among predictors without requiring transformations or assumptions of linearity.

RTA, however, can be sensitive to overfitting. Therefore, prior to performing the RTA, we reduced the dimensionality of correlated geomorphological and land-use variables through two Principal Component Analyses (PCA): one for lake and catchment morphometric, topographic and geomorphological attributes (LP, LA, LP:LA, SD, CA, LA:CA, MCS), hereafter PCA_{geo}, and another for catchment land-use properties (CAA, CARel, CAA:LA, CAA:LP), hereafter PCA_{lu}. PCA was used to summarize the main environmental gradients represented by these two classes of geomorphological and land-use associated variables and to reduce

multicollinearity among predictors. The first two axes of each PCA were retained and included as explanatory variables in the RTA. All statistical analyses were performed in the R statistical environment (R Core Team 2026). Principal component analyses were conducted using the *vegan* package (Oksanen et al. 2026), and RTA was fitted using the *rpart* package (Therneau and Atkinson 2026).

RESULTS

The studied lakes encompassed broad environmental gradients in both in-lake and out-lake predictors (Table 1). Among in-lake variables, DOC ranged from 3.4 to 822.5 mg L^{-1}, pCO_2 ranged from 6.4 to 47256.3 µatm, Chl-a ranged from 0.3 to 628.3 µg L^{-1}, TDP ranged from 0.02 to 1.04 mg L^{-1}, and Secchi depth ranged from 0.01 to 2.75 m. Out-lake variables also varied substantially among systems, including cumulative precipitation during the two-year period preceding sampling, which ranged from 58.4 to 1239.6 mm, and catchment relative anthropogenic area (CARel), which ranged from 0 to 100%.

Table 1

Description of predictor variables used in the Regression Tree Analysis (RTA) to explain variation in seston C:P stoichiometry across tropical lakes. For each variable, we provide its ecological rationale, expected mechanisms linking it to seston C:P stoichiometry, data source, and measurement or estimation method. Rationale emphasizes how each predictor may influence seston C:P through effects on nutrient availability, inorganic carbon supply, phytoplankton physiology or composition, and allochthonous inputs. Summary statistics are presented as mean ± standard deviation (SD), followed by minimum and maximum values in parentheses

Variables	**Rationale**	**Source**	**Measurement and/or method**	**Mean ± SD (min - max)**
In-lake predictors				
Dissolved organic carbon (mg l^{-1})	Dissolved organic carbon represents the pool of allochthonous dissolved carbon entering lakes and can influence seston C:P indirectly through multiple pathways. DOC can reduce light availability via water browning, potentially constraining phytoplankton production and altering nutrient uptake dynamics (Jansson et al. 2000; Karlsson et al. 2009). It may also stimulate heterotrophic microbial activity, potentially modifying nutrient recycling and competition with phytoplankton (Cotner and Biddanda, 2002). However, if DOC is not retained as an important predictor, this suggests that light-mediated or microbial pathways are not dominant drivers of seston C:P variation in these systems.	Our survey	DOC concentrations were quantified using a high-temperature combustion Total Organic Carbon Analyzer (TOC-V, Shimadzu) coupled to a TN analyzer module, following standard infrared detection protocols for dissolved carbon fractions	36.2 ± 84.2 (3.4–822.5)
Partial pressure of CO_2 (µatm)	Partial pressure of CO_2 reflects the availability of dissolved inorganic carbon (DIC), a key resource for phytoplankton. Higher pCO_2 is expected to increase carbon availability relative to phosphorus, potentially increasing seston C:P through shifts in phytoplankton carbon assimilation and allocation strategies (Verschoor et al. 2013).	Our survey	Calculated from pH and alkalinity with corrections for water temperature and wind velocity (Weiss, 1974; Cole et al. 1994)	10913 ± 11169.1 (6.4–47256.3)

Variables	Rationale	Source	Measurement and/or method	Mean ± SD (min - max)
Chlorophyll-a ($\mu g\ L^{-1}$)	Chlorophyll-a is a proxy for phytoplankton biomass. While biomass can influence seston stoichiometry, particularly through shifts in nutrient demand and recycling, the absence of chlorophyll-a as a key predictor suggests that variation in seston C:P is not primarily driven by phytoplankton quantity. Instead, it points toward mechanisms related to physiological plasticity or changes in species composition (Boyer et al. 2009; Sterner and Elser, 2002).	Our survey	Chlorophyll-a was extracted from filtered water samples using 95% ethanol and quantified spectrophotometrically at 665 and 750 nm following Jespersen and Christoffersen (1987).	63.1 ± 116.3 (0.3–628.3)
Total dissolved phosphorus ($mg\ L^{-1}$)	Dissolved phosphorus represents a key limiting nutrient in freshwater ecosystems and is expected to directly regulate seston C:P stoichiometry. Increased phosphorus availability typically reduces C:P by alleviating nutrient limitation and promoting the production of P-rich phytoplankton biomass (Elser et al. 2000; Sterner and Elser, 2002).	Our survey	TDP was measured after persulfate digestion (Valderrama, 1981) followed by colorimetric determination using the molybdenum blue method (Murphy and Riley, 1962).	0.23 ± 0.20 (0.02–1.04)
Secchi disc depth (m)	Secchi depth is a proxy for water transparency and light availability, which can influence phytoplankton growth and stoichiometry. Reduced light availability can constrain primary production and alter carbon fixation relative to nutrient uptake (Wetzel, 2001; Kirk, 2011). However, if Secchi depth is not retained as an important predictor, this suggests that variation in light availability is unlikely to be a dominant mechanism structuring seston C:P across systems.	Our survey	Measured in situ at midday using a Secchi disk at a standardized location where total water depth exceeded Secchi depth to ensure reliable readings.	0.76 ± 0.68 (0.01–2.75)
Geomorphological predictors of lake-catchment system				

Variables	Rationale	Source	Measurement and/or method	Mean ± SD (min - max)
Lake perimeter - LP (km)	It represents the potential connectivity of the lake with its surrounding terrestrial habitat and the relative extent of littoral region to the whole lake ecosystem, which can affect the magnitude of contribution of terrestrial allochthonous material and littoral vegetation detritus typically enriched in carbon relative to phosphorus to lake seston (Håkanson, 2005; Vanni et al. 2011).	Our survey and TOPODATA	Derived from lake polygon shapefiles obtained from satellite imagery and processed in ArcGIS 10.5.1 (ESRI, 2017).	5.31 ± 10.10 (0.22–54.45)
Lake area – LA (km^2)	It regulates the balance between external inputs and internal processes. Larger lakes are expected to be less influenced by terrestrial inputs per unit area but more susceptible to wind-driven sediment resuspension, which can introduce particulate material and nutrients into the water column, potentially affecting seston C:P (Fee, 1979; Scheffer, 2004).	Our survey and TOPODATA	Calculated from GIS-based polygon shapefiles using lake's polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017).	0.78 ± 2.07 (0.002–132.86)
LP:LA ratio	It represents the relative connectivity between lake size and surrounding terrestrial habitat. Higher values indicate higher edge-to-size ratios, suggesting stronger terrestrial influence and potentially greater contributions of detrital material to seston (Håkanson, 2005; Setubal et al. 2026).	Our survey and TOPODATA	Calculated as lake perimeter divided by lake area using lake's polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017).	0.020 ± 0.017 (0.003–0.098)
Catchment area – CA (km^2)	Catchment area determines the spatial extent of terrestrial inputs to lakes. Larger catchments are expected to harbor higher amounts of nutrients and organic matter and therefore, contribute with larger fluxes of these materials to lakes,	Our survey and TOPODATA	Delineated using lake's polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017).	130.25 ± 375.87 (0.14–2049.3)

Variables	Rationale	Source	Measurement and/or method	Mean ± SD (min - max)
	potentially altering seston C:P (Vanni et al. 2011).			
LA:CA ratio	Represents the relative influence of catchment-derived inputs per unit of lake area. Lower values suggest stronger influence of terrestrial subsidies relative to lake size, potentially increasing variability in seston stoichiometry (Håkanson, 2005; Setubal et al. 2026).	Our survey and TOPODATA	Calculated as the ratio between lake area and catchment area using lake's polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017).	0.0704 ± 0.1297 (0.0003–0.7186)
Shoreline development	It measures how the shape of a lake approximates to or deviates from a perfect circle. The value of 1 indicates the lake shape resembles a perfect circle and higher values indicate the lake morphometry resembles more complex shapes. Higher and lower values indicate lakes are more and less influenced by littoral and riparian regions, respectively (Håkanson, 2005)	Our survey and TOPODATA	The index is calculated by the formula $\mathrm{SD} = \frac{L}{2\sqrt{\pi A}}$ where L is lake perimeter and A is lake area. Lake's polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017).	1.8 ± 0.8 (1.0–5.3)
Mean catchment slope (°)	It influences hydrological transport processes. Steeper catchments are expected to increase erosion and runoff, enhancing the delivery of particulate and dissolved materials to lakes, potentially altering seston C:P (Kamenik et al. 2001).	Our survey and TOPODATA	Derived from 30-m resolution DEM (TOPODATA) using slope functions in ArcGIS.	2.1 ± 1.2 (0.5–6.7)
Land use properties predictors				
Catchment anthropic area - CAA (km^2)	It is a proxy of the potential absolute amount of the land-use mediated allochthonous input delivered to the lake. Catchments with larger anthropogenic (human-impacted) areas tend to deliver higher loads of nutrients (Foley et al. 2005), potentially altering the	Mapbiomas 3.0	Calculated from MapBiomas land-use data (Collection 3) as the sum of areas classified as agriculture, pasture, and urban land within each catchment using ArcGis 10.5.1. (ESRI, 2017)	53.27 ± 140.23 (0.0–698.16)

Variables	Rationale	Source	Measurement and/or method	Mean ± SD (min - max)
	stoichiometry of the seston in the aquatic environment.			
Catchment relative anthropic area CArel (%)	Represents the proportional dominance of anthropogenic land use in catchment. It can affect the quality and quantity of land-use mediated transport of particulate and dissolved terrestrial material to lakes (Foley et al. 2005).	Mapbiomas 3.0	Computed as the percentage of total catchment area classified as anthropogenic land use using MapBiomas land-use data (Collection 3) ArcGis 10.5.1. (ESRI, 2017).	60.6 ± 27.1 (0.0–100)
CAA:LA	It is a proxy of the absolute amount of land-use mediated allochthonous input that can reach the lake per unit of lake area.	Mapbiomas 3.0, our survey and TOPODATA	It is calculated by the ratio of catchment anthropic area to lake area.	107.7 ± 253.1 (0.0–1878.1)
CAA:LP	It is a proxy of the absolute amount of land-use mediated allochthonous input that can reach the lake per unit of lake perimeter.	Mapbiomas 3.0, our survey and TOPODATA	It is calculated by the ratio of catchment anthropic area to lake perimeter.	6138.0 ± 12699.2 (0.0–83476.5)
Climate predictor				
Total precipitation (mm)	Influences the potential amount of nutrients and matter entering the aquatic ecosystems due to runoff of allochthonous material via subsurface and groundwater flow. May also increase the volume of lakes causing the dilution of nutrients.	INMET	Monthly cumulative precipitation from September 2010 to September 2012.	477.01 ± 270.8 (58.4–1239.6)

The PCA_{geo} summarized the main geomorphological gradients of the lake–catchment systems (Table 2a; Fig. 2a). The first two axes of the PCA_{geo} together explained 70.97% of the variance among lakes. The first axis explained 52.38% of the variance and was strongly negatively correlated with lake perimeter (LP, r = − 0.9595), shoreline development (SD, r = − 0.9085), catchment area (CA, r = − 0.8622), lake area (LA, r = − 0.8546), and mean catchment slope (MCS, r = − 0.5175). Thus, lower scores on PCA_{geo} axis 1 were associated with lakes with larger perimeter, larger lake area, larger catchment area, greater shoreline development, and steeper catchments. The second axis explained 18.59% of the variance and was mainly associated with the lake area-to-catchment area ratio (LA:CA, r = 0.8707) and the lake perimeter-to-lake area ratio (LP:LA, r = − 0.6377), indicating that this axis represented variation in the relative size and shape of lakes in relation to their catchments.

Table 2

Pearson correlation coefficients between the original environmental variables and the first two axes of the two Principal Component Analyses used to summarize out-lake predictors included in the Regression Tree Analysis. Panel (a) shows the PCA of geomorphological properties of the lake–catchment system (PCAgeo), including lake area (LA), catchment area (CA), lake area-to-catchment area ratio (LA:CA), lake perimeter (LP), lake perimeter-to-lake area ratio (LP:LA), shoreline development (SD), and mean catchment slope (MCS). Panel (b) shows the PCA of catchment land-use properties (PCAlu), including catchment anthropogenic area (CAA), relative anthropogenic area in the catchment (CARel), catchment anthropogenic area-to-lake area ratio (CAA:LA), and catchment anthropogenic area-to-lake perimeter ratio (CAA:LP). Explained variance indicates the percentage of total variance among lakes represented by each PCA axis. Bold values are significant ($p < 0.05$), Pearson's r correlation coefficients indicating the direction and strength of correlations between original variables and PCA axes

a) PCA*geo*	**Pearson's coefficient**							
	LA	**CA**	**LA:CA**	**LP**	**LP:LA**	**SD**	**MCS**	**Explained variance**
PCA1	**-0.8546**	**-0.8622**	0.1328	**-0.9595**	0.4017	**-0.9085**	**-0.5175**	52.38%
PCA2	0.19	-0.1346	**0.8707**	0.0761	**-0.6377**	-0.1557	-0.2289	18.59%
b) PCA*lu*	CAA	CARel	CAA:LA	CAA:LP				Explained variance
PCA1	**0.6739**	-0.0717	**0.8288**	**0.9721**				52.28%
PCA2	-0.4072	**0.9028**	0.3068	0.0873				27.07%

The PCA_{lu} summarized the main gradients of catchment land-use properties (Table 2; Fig. 2b). The first two axes of the PCA_{lu} together explained 79.35% of the variance among lakes. The first axis explained 52.28% of the variance and was strongly positively correlated with the catchment anthropogenic area-to-lake perimeter ratio (CAA:LP, r = 0.9721), the catchment anthropogenic area-to-lake area ratio (CAA:LA, r = 0.8288), and catchment anthropogenic area (CAA, r = 0.6739). Therefore, higher scores on PCA_{lu} axis 1 were associated with catchments with larger absolute anthropogenic areas and greater anthropogenic area relative to lake size and perimeter. The second axis explained 27.07% of the variance and was strongly positively correlated with catchment relative anthropogenic area (CARel, r = 0.9028), indicating that higher scores on this axis represented lakes whose catchments had a greater proportional dominance of anthropogenic land use.

The RTA explained 49.61% of the variance in seston C:P ratio across lakes (Fig. 3). The first split in the tree was determined by cumulative precipitation during the two-year period preceding sampling, separating lakes with precipitation below 882 mm from those with precipitation equal to or above this threshold. Only cumulative precipitation, TDP, pCO_2, and PCA_{lu} axis 2 were retained as splitting variables in the final tree. In contrast, PCA_{geo} axes, PCA_{lu} axis 1, DOC, Chl-a, and Secchi depth were not retained as relevant predictors in the final RTA model.

Among lakes with cumulative precipitation equal to or above 882 mm, TDP (node 3) was the only additional splitting variable retained in the tree (Fig. 3). In this high-precipitation branch, lakes with TDP < 0.1 mg L^{-1} (terminal node 6) had a mean seston C:P ratio of 1252.08 ± 286 (n = 7), whereas lakes with TDP ≥ 0.1 mg L^{-1} (terminal node 7) had the highest mean seston C:P ratio observed in the tree (8355.35 ± 327; n = 5). Thus, the

highest seston C:P ratios occurred in lakes combining high cumulative precipitation and high TDP concentration.

Among lakes with cumulative precipitation below 882 mm, pCO_2 (node 2) was the next variable retained by the tree (Fig. 3). Lakes with $pCO_2 \geq 32031.5$ µatm formed a terminal node with relatively high seston C:P ratios (node 5; 1459.94 ± 238; n = 5). In contrast, lakes with $pCO_2 < 32031.5$ µatm were further split by PCA_{lu} axis 2 (node 4). Within this subset, lakes with PCA_{lu} axis 2 ≥ 1.2 (terminal node 9) also showed relatively high seston C:P ratios (1103.96 ± 769; n = 5), whereas lakes with PCA*lu* axis 2 < 1.2 were further partitioned by a lower pCO_2 threshold of 14467.1 µatm (node 8). The lowest mean seston C:P ratio occurred in lakes with cumulative precipitation < 882 mm, $pCO_2 < 32031.5$ µatm, PCA_{lu} axis 2 < 1.2, and $pCO_2 < 14467.1$ µatm (terminal node 10; 414.39 ± 29; n = 59). Lakes in the same branch but with $pCO_2 \geq 14467.1$ µatm had higher seston C:P ratios (terminal node 11; 767.33 ± 98; n = 14).

DISCUSSION

Our results reveal a clear hierarchical structure in the environmental drivers of seston C:P stoichiometry across these tropical shallow lakes. We hypothesized that broad-scale climatic and lake–catchment variables would exert stronger control over seston stoichiometry than local limnological conditions, because they integrate hydrological, geomorphological and land-use processes operating at larger spatial and temporal scales. This expectation was only partially supported. Cumulative precipitation during the two years preceding sampling was the first variable retained by the RTA, indicating that climate-related hydrological forcing provides the primary environmental template structuring seston C:P ratio across the studied lakes. However, in-lake variables were also important, as TDP and *p*CO2 acted as secondary predictors within specific precipitation-defined branches, and land use contributed to explaining seston C:P ratio variation under a restricted set of conditions in lakes with lower precipitation. This hierarchical pattern is consistent with the view that lake biogeochemistry emerges from cross-scale interactions between climatic forcing, watershed inputs and internal ecological processes (Carpenter et al. 1998; Chiandet and Xenopoulos 2011; Vanni et al. 2011; Soranno et al. 2015; Nobre et al. 2020).

The dominant role of precipitation highlights the importance of hydrological connectivity in regulating seston stoichiometry. Rainfall controls runoff intensity, hydrological exchange between catchments and lakes, and the transport of dissolved nutrients, organic matter and suspended particles to aquatic ecosystems (Carpenter et al. 1998; Vanni et al. 2011; Rose et al. 2017; Nobre et al. 2020). In tropical shallow lakes, such hydrological effects are likely amplified because low depth increases the relative influence of catchment inputs, sediment–water interactions and water-level fluctuations on pelagic conditions. Previous studies have shown that precipitation can influence lake water quality and plankton dynamics by altering nutrient availability, turbidity, residence time and the timing of phytoplankton responses to nutrient pulses (Collins et al. 2019; Liu et al. 2024; Lau et al. 2021; Shuvo et al. 2021). The emergence of precipitation as the first split in our regression tree therefore suggests that seston C:P ratios are governed not only by local, instantaneous limnological conditions, but also by the broader hydrological context in which each lake is embedded.

Among lakes experiencing higher cumulative precipitation, TDP was the only additional variable retained by the tree, and the highest seston C:P ratios occurred in lakes combining precipitation ≥ 882 mm and TDP ≥ 0.1 mg L^{-1}. This result is notable because greater phosphorus availability is generally expected to reduce phytoplankton C:P ratios by alleviating phosphorus limitation and favoring P-rich biomass (Sterner and Elser 2002; Hessen 2006; Andersen et al. 2025). The occurrence of the highest seston C:P ratios under high TDP therefore, suggests that TDP is not acting here solely as a proxy for phytoplankton phosphorus limitation. Instead, elevated TDP under wetter conditions may indicate stronger hydrological inputs from the catchment, where dissolved phosphorus can arrive together with carbon-rich suspended organic matter, fine detritus and mineral particles. Because bulk seston integrates phytoplankton, heterotrophic microorganisms, detrital particles and inorganic suspended material, an increased contribution of non-algal particles can elevate seston C:P ratio even when dissolved phosphorus concentrations are high (Hessen 2006; Chiandet and Xenopoulos 2011; Vanni et al. 2011; Baltodano et al. 2022).

This interpretation is consistent with the composite nature of seston. Although phytoplankton often represents the dominant biological component of lake seston, seston C:P ratio does not necessarily track phytoplankton cellular stoichiometry directly; it may also reflect shifts in the relative contribution of detrital material, suspended sediments, bacteria and other particulate fractions (Hessen 2006; Urabe 1995; Moorthi et al. 2017). Our sampling design, based on subsurface limnetic samples collected from the central region of each lake, likely minimized direct littoral and benthic influences, but cannot entirely exclude the contribution of fine particulate organic detritus or mineral particles to bulk seston. This is particularly relevant in shallow systems, where sediment resuspension and catchment-derived inputs can contribute substantially to suspended particulate matter (Thornton et al. 1990; Kiage et al. 2007). The extreme C:P ratio values observed in the high-precipitation, high-TDP lakes may therefore reflect a combination of hydrological transport, dissolved phosphorus supply and shifts in seston composition, rather than a purely phytoplankton physiological response.

At the same time, phytoplankton-based mechanisms remain important for interpreting seston C:P stoichiometry. Ecological stoichiometry theory predicts that phytoplankton C:P ratios vary with resource availability, growth rate and cellular allocation strategies (Elser et al. 2000; Sterner and Elser 2002; Geider and La Roche 2002). Phytoplankton communities can respond to environmental gradients through physiological plasticity within taxa, changes in nutrient uptake and storage, or species turnover among taxa differing in elemental composition and resource-acquisition strategy (Litchman and Klausmeier 2008; Yvon-Durocher et al. 2017; Hillebrand et al. 2022). Precipitation may therefore influence seston stoichiometry indirectly, by reshaping nutrient regimes and the environmental filters that determine phytoplankton composition. Recent work on these same lakes showed that phytoplankton communities are frequently phosphorus-limited and that phosphorus availability influences the relative success of mixotrophic taxa (Costa et al. 2024). Because mixotrophic algae can differ from strictly autotrophic taxa in their nutrient-acquisition strategies and elemental composition, shifts in their relative abundance could contribute to variation in seston C:P ratio even without large changes in total phytoplankton biomass (Mitra et al. 2014; Moorthi et al. 2017; Costa et al. 2024).

Among lakes with lower cumulative precipitation, pCO_2 emerged as an important predictor of seston C:P ratio. Carbon dioxide is the main inorganic carbon source for phytoplankton photosynthesis, and variation in pCO_2 can influence carbon acquisition, carbon-fixation efficiency and cellular elemental composition (Urabe et al. 2003; Beardall et al. 2009; Raven et al. 2011). In our RTA, lakes with low precipitation and $pCO_2 \geq$ 32031.5 µatm had relatively high seston C:P ratios, while within the lower-pCO_2 branch a second pCO_2 threshold further separated lakes with the lowest and the higher C:P ratios. Because the carboxylation efficiency of RuBisCO increases with the availability of CO_2 relative to O_2, higher pCO_2 can allow phytoplankton to fix proportionally more carbon per unit of phosphorus assimilated (Morell et al. 1992), and comparable pCO_2-driven increases in the carbon content of seston and grazers have been reported in experimental and observational studies (Urabe et al. 2003; Rossoll et al. 2012; Katkov and Fussmann 2023). This pattern suggests that inorganic carbon availability can modulate seston stoichiometry in drier systems, where longer water residence times, stronger evaporative concentration and more intense internal nutrient recycling may shift the balance between carbon fixation and phosphorus assimilation (They et al. 2017).

The fact that Secchi depth, DOC and Chl-a were not retained in the RTA helps to constrain the most plausible mechanisms. Secchi depth and DOC are commonly associated with underwater light availability, either through turbidity or water colour, and light availability can shape phytoplankton stoichiometry through the light:nutrient balance (Sterner et al. 1997; Dickman et al. 2006). The absence of either variable from the final model suggests that variation in the light climate was not the dominant pathway structuring seston C:P ratio across these lakes. Similarly, the exclusion of Chl-a indicates that variation in phytoplankton biomass alone was insufficient to explain the observed stoichiometric patterns. Together, these results point toward mechanisms related to phytoplankton physiological plasticity and species composition, inorganic carbon availability, and the relative contribution of non-algal seston fractions, rather than to simple changes in algal biomass or light limitation.

Land use also contributed to explaining seston C:P ratio variation, but only within the low-precipitation branch and after pCO_2 had already partitioned the data. Specifically, PCA_{lu} axis 2, which was strongly associated with the relative proportion of anthropogenic area in the catchment (CARel, r = 0.90; Table 2), separated lakes with higher seston C:P ratios from those with lower values. Anthropogenic land use can alter lake stoichiometry by changing erosion rates, sediment transport, nutrient export and the quantity and quality of organic matter delivered to aquatic ecosystems (Foley et al. 2005; Chiandet and Xenopoulos 2011; Vanni et al. 2011). If land-use effects operated solely through phosphorus enrichment, a higher anthropogenic influence would be expected to reduce seston C:P ratio. However, anthropogenic catchments can also increase the delivery of suspended particles and terrestrial detrital material (Junger et al. 2019), potentially raising bulk seston C:P ratio when carbon-rich particulate inputs are large relative to the phosphorus incorporated into algal biomass. The conditional position of PCA_{lu} axis 2 in the tree therefore suggests that land-use effects on seston stoichiometry are mediated by the broader hydrological and biogeochemical context, rather than acting uniformly across all lakes (Chiandet and Xenopoulos 2011; Soranno et al. 2015; Rose et al. 2017).

In contrast, the geomorphological properties summarized by PCA_{geo} were not retained as predictors in the RTA. This indicates that variation in lake perimeter, lake area, catchment area, shoreline development, the

lake area-to-catchment area ratio and mean catchment slope did not explain seston C:P ratio once precipitation, TDP, pCO_2 and land use were accounted for. This does not imply that lake–catchment geomorphology is unimportant for lake functioning in general. Rather, in this dataset its effects may have been weaker than those of hydrological forcing and land-use intensity or may already be incorporated indirectly through the precipitation and land-use gradients. Indeed, about 70% of the studied catchments had more than half of their area under anthropogenic land use, which may have reduced the relative importance of natural landscape gradients and amplified the influence of land use itself (Rose et al. 2017). Previous landscape-limnology studies have similarly shown that the importance of morphometric and watershed variables depends on spatial scale, hydrological connectivity, lake type and the degree of human modification of the catchment (Read et al. 2015; Rose et al. 2017; Soranno et al. 2015; Nobre et al. 2020).

Some limitations should be considered when interpreting these potential mechanisms. First, our response variable was bulk seston C:P ratio, and we did not quantify the relative contributions of phytoplankton, bacteria, detritus and inorganic suspended particles to seston; we therefore cannot definitively separate physiological changes in phytoplankton from shifts in seston composition. Second, although Chl-a was included as a proxy for phytoplankton biomass, we did not directly assess phytoplankton taxonomic or functional composition in this analysis. Third, our survey was based on a single dry-season sampling campaign, whereas precipitation was represented by cumulative rainfall over the two years preceding sampling; the precipitation effect detected here should therefore be interpreted as a hydrological legacy or regional climatic template rather than as an immediate response to a rainfall event, and plankton responses to individual rainfall pulses can occur with a lag of several weeks (Liu et al. 2024). Despite these limitations, the RTA explained nearly half of the variance in seston C:P ratio across lakes, indicating that the combination of precipitation, phosphorus availability, inorganic carbon supply and land use captures major axes of stoichiometric variation across these tropical shallow lakes.

Overall, our findings show that seston stoichiometry in tropical shallow lakes emerges from the interaction between climatic forcing, internal lake biogeochemistry and watershed processes. Precipitation establishes the broad hydrological context that regulates material exchange between catchments and lakes; within this context, phosphorus availability and inorganic carbon supply shape stoichiometric variation, while land use modulates seston C:P ratio under specific hydrological conditions. These results reinforce the need to interpret seston C:P ratio not only as a signal of phytoplankton nutrient limitation, but also as an integrated property of lake–catchment systems in which hydrology, land use, carbon availability and particulate inputs jointly determine the elemental composition of suspended material.

Declarations

Competing Interests

The author Rafael Dettogni Guariento is a member of the editorial board of the Aquatic Ecology.

Author Contribution

AC and ASM conceptualized the study question; AC, LSC and CRC designed the field samplings. ASM wrote the main manuscript text with large inputs of AC. CRC and LBQ conducted the field samplings and laboratorial analysis. ASM and RLGN analyzed the data. LSC and AMA get funding. All authors reviewed the manuscript.

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Data Availability

Data used in this study will be available upon reasonable request to the corresponding author.

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Figures

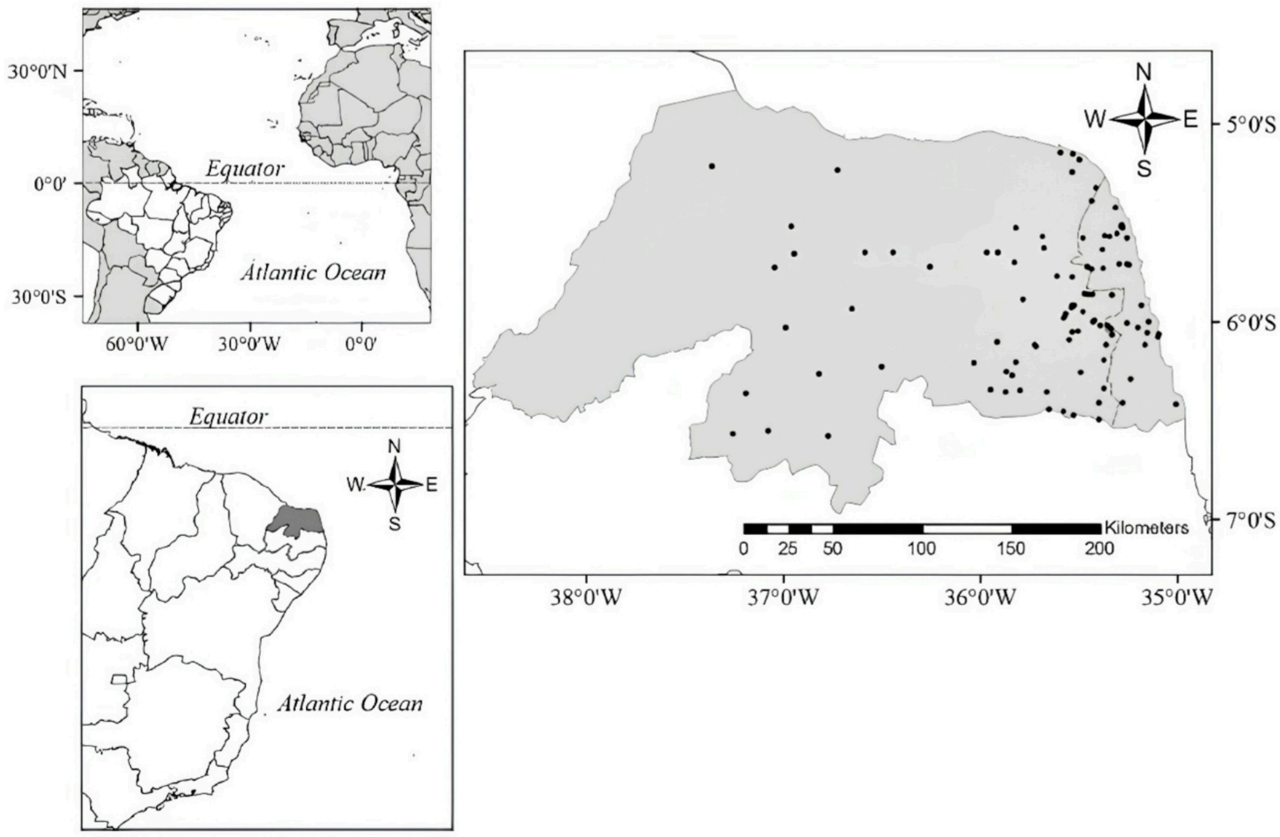


Figure 1

Map of the study area showing the 95 lentic aquatic systems distributed across the state of Rio Grande do Norte, in northeast Brazil. The dotted line on the map indicates the transition between the tropical humid (on the right) and semi-arid regions (on the left)

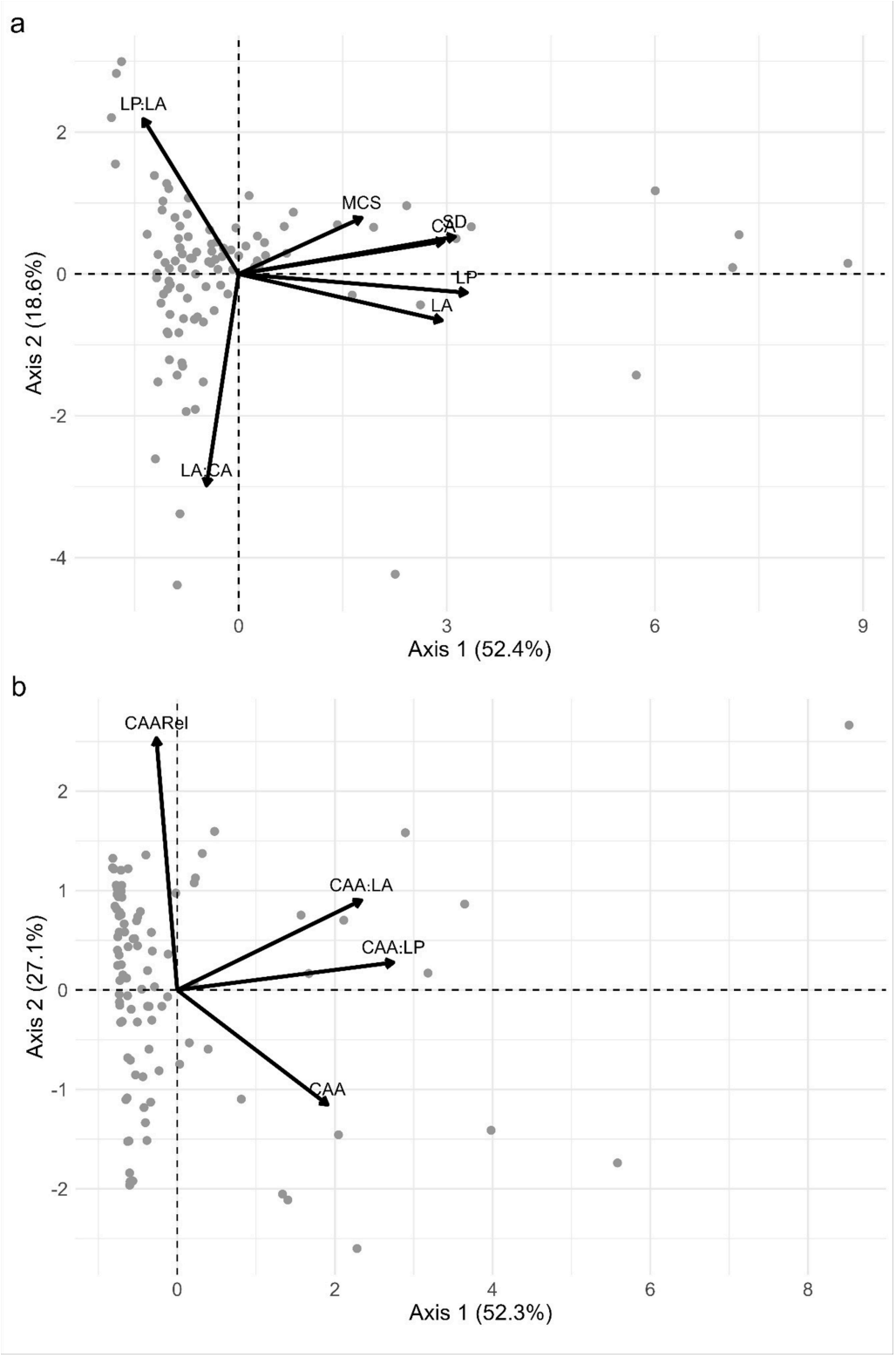


Figure 2

Principal Component Analysis biplots summarizing out-lake predictors associated with geomorphological and land-use properties of the lake–catchment systems. (a) PCA of geomorphological properties of the lake–catchment system (PCA_{geo}), including lake area (LA), catchment area (CA), lake area-to-catchment area ratio (LA:CA), lake perimeter (LP), lake perimeter-to-lake area ratio (LP:LA), shoreline development (SD), and mean catchment slope (MCS). The first and second axes explained 52.38% and 18.59% of the variance

among lakes, respectively. (b) PCA of catchment land-use properties (PCA_{lu}), including catchment anthropogenic area (CAA), relative anthropogenic area in the catchment (CARel), catchment anthropogenic area-to-lake area ratio (CAA:LA), and catchment anthropogenic area-to-lake perimeter ratio (CAA:LP). The first and second axes explained 52.28% and 27.07% of the variance among lakes, respectively. Points represent lakes, and vectors indicate the direction and strength of correlations between original variables and PCA axes

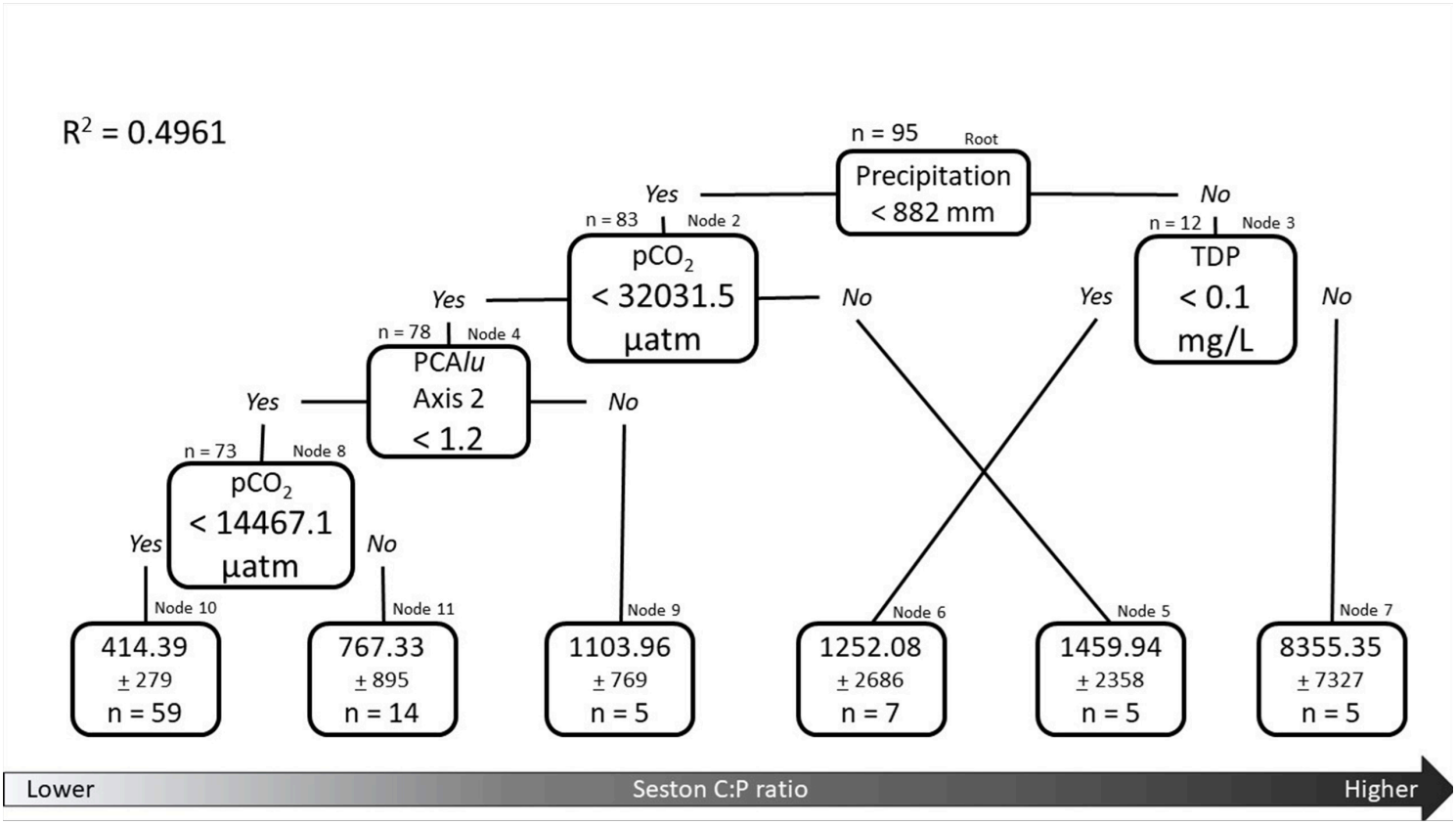


Figure 3

Regression Tree Analysis (RTA) explaining variation in the seston carbon-to-phosphorus molar (C:P) ratio across tropical lakes as a function of in-lake and out-lake environmental predictors. Internal nodes indicate the environmental variables, the number of lakes and threshold values that best partition variation in seston C:P ratio. Nodes 10, 11, 9, 5, 6 and 7 represent terminal nodes and show the mean seston C:P ratio, standard deviation, and number of lakes within each group. Branches labeled “Yes” indicate lakes satisfying the splitting condition, whereas branches labeled “No” indicate lakes not satisfying the condition. Precipitation represents accumulated rainfall during the two-year period preceding sampling; TDP is total dissolved phosphorus concentration; pCO_2 is the partial pressure of dissolved carbon dioxide in water; and PCA_{lu} Axis 2 is the second axis of the PCA summarizing catchment land-use properties. The arrow at the bottom indicates the gradient from lower to higher seston C:P ratios among terminal nodes