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Nitrogen and phosphorus uptake dynamics in anthropized and conserved Caatinga dry forests

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ABSTRACT

Understanding human impacts on drylands is crucial in a global scenario of forest degradation and biodiversity loss. This study analyzed foliar concentrations of nitrogen (N) and phosphorous (P) in the Brazilian seasonally dry tropical forests (Caatinga). Foliar patterns of N, P, and the N/P ratio were assessed both within and among botanical families. To do this, 10 plots were established in an anthropized area and 10 in a conserved area. Within each plot, leaves from all tree species and soil samples from four random points were collected. Stoichiometric analyses were performed on the leaves of 136 trees from 14 botanical families. Significant differences were observed in soil P concentrations, organic matter content, and cation exchange capacity, with the highest values found in the conserved area. Foliar N and P concentrations and N/P were also higher in the conserved area for the F+ (nitrogen-fixing Fabaceae), F- (non-nitrogen-fixing Fabaceae), and NF (non-Fabaceae) groups, indicating greater efficiency in nutrient retention and cycling. When comparing species found in both areas, *Aspidosperma pyrifolium* (NF), *Bauhinia forficata* (F-), and *Mimosa ophthalmocentra* (F+) showed significant differences in foliar N concentrations and foliar P (for *A. pyrifolium* and *B. forficata* only). Degradation of the Caatinga directly impacts nutrient cycling.

1. Introduction

Nutrients such as nitrogen (N) and phosphorus (P) are among the most abundant in plants, playing a crucial role in regulating plant growth and altering species composition across different environments (Wang et al., 2023). N and P are the macronutrients most commonly limiting to plant growth in tropical ecosystems, as they are involved in several essential metabolic processes and serve as structural components of biomolecules like nucleic acids, proteins, and phospholipids, among others (Liu et al., 2019). Consequently, their uptake affects plant physiology, biogeochemical cycles, and community ecology (Chang et al., 2022; Lin et al., 2022). Foliar N and P analyses can be used as indicators of nutrient status, providing insights into net primary productivity and organic matter decomposition (Yan et al., 2022; Dynarski et al., 2023).

Understanding the dynamics of foliar N and P uptake from plant organic matter is thus crucial for identifying patterns of mineral nutrition in tropical plants. This knowledge is important for implementing forest management practices that minimize organic matter loss in forests, particularly in a global context of degradation and loss of biological diversity. In Brazil, seasonally dry tropical forests include semi-deciduous seasonal forests within the Atlantic Forest domain and semiarid forests/woodlands within the Brazilian Caatinga, located in the

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northeast region (de Queiroz et al., 2017). The Caatinga forms a vegetation mosaic, representing the largest tropical semiarid ecoregion in South America, with a high degree of endemism (Moro et al., 2016; Fernandes et al., 2020). Climate in the Caatinga region is characterized by a long dry season and irregular rainfall, with annual precipitation ranging from 250 to 800 mm (Falcão et al., 2022). The most abundant plant families in the Caatinga biome include Fabaceae, Euphorbiaceae, Poaceae, Asteraceae, Rubiaceae, and Malvaceae, with some Myrtaceae tree species, that might be dominant in montane areas (de Queiroz et al., 2017).

The intensive and frequent land use and exploitation of forest resources in the Caatinga have led to drastic reductions in vegetation cover, resulting in areas undergoing desertification (Silva et al., 2019; Araujo et al., 2023; Refati et al., 2023). In addition to clear-cutting and burning, the Caatinga has historically experienced continuous low-intensity use, with selective cutting of wood for domestic fuel, causing degradation of the standing forest, termed chronic anthropogenic disturbance (Ribeiro et al., 2015). This type of disturbance strongly alters species diversity, ecological processes, and ecosystem services (Antongiovanni et al., 2020; Menezes et al., 2024), with consequences for biogeochemical cycles (Silva et al., 2021).

Most of Caatinga's soils are nutrient-poor, mainly deficient in N and P (Gava et al., 2022; Menezes et al., 2012). The stoichiometry of N and P serves as a key indicator of plant nutrient utilization and is closely related to species adaptation strategies (Tian et al., 2018; Chang et al., 2022). The limitation of these elements in terrestrial ecosystems significantly affects plant growth and productivity (Yan et al., 2018; Tong et al., 2020). Therefore, understanding the dynamics of nutrient uptake and the impacts of disturbances on this process is crucial for the management and restoration of tropical dry forests. This study aimed to (1) identify foliar patterns of N and P concentrations, and the N/P ratio in tree species of different botanical families from the Caatinga; (2) evaluate foliar N and P concentrations in the Caatinga, comparing anthropized vs. conserved areas. The findings may also enhance our understanding of plant nutrient limitations in anthropized areas at a regional scale, providing information for restoration and management in degraded areas and tropical drylands.

2. Materials and methods

2.1. Study sites

This study was conducted in an anthropized area located in the Dom Hélder Câmara settlement, situated in the Girau do Ponciano municipality (Latitude −9.884167; Longitude −36.828889; latitude 244 m), and in a conserved area located within the Experimental Station of the Institute for Innovation for Sustainable Rural Development of Alagoas (EMATER), in the municipality of Santana do Ipanema, in the Sertão Alagoano region (Latitude −9.378333; Longitude −37.245278; Altitude 250 m) (Fig. 1). Both anthropized and conserved areas are situated in seasonally dry tropical forests of the Caatinga domain, in the semiarid region of northeastern Brazil. The region is characterized by a seasonal tropical climate, with a dry spring/summer transition and a rainy autumn/winter, with minimal and maximal temperatures of 21 °C and 38 °C, respectively. The average annual precipitation ranges from 600 mm to 800 mm (Barros et al., 2012).

2.2. Field collections

In total, 20 sampling plots (10 m × 10 m) were established across the study sites (Fig. 2), with 10 plots in each area, preferably where vegetation cover was denser. The location of the first plot was randomized, and subsequent plots were set at 5-m intervals. The samplings were conducted during September 2017, at the beginning of the dry season (i.e., end of the rainy season) in both anthropized (A) and conserved (C) areas. Each plot represented one field repetition. Leaves were collected from all plant species within each plot, selecting one individual per species. The collected leaves were, if possible, fully expanded, undamaged by herbivores or pathogens, from adult individuals, and located in the middle of the tree canopies.

All leaf samples were placed in paper bags and dried in an oven at 65 °C for 72 h. Additionally, specimens of the collected plant species were prepared for botanical identification. All plant species were then identified by comparison with other specimens in the herbarium of the Federal University of Alagoas (UFAL) – Arapiraca *campus* and of the Federal Rural University of Pernambuco (UFRPE).

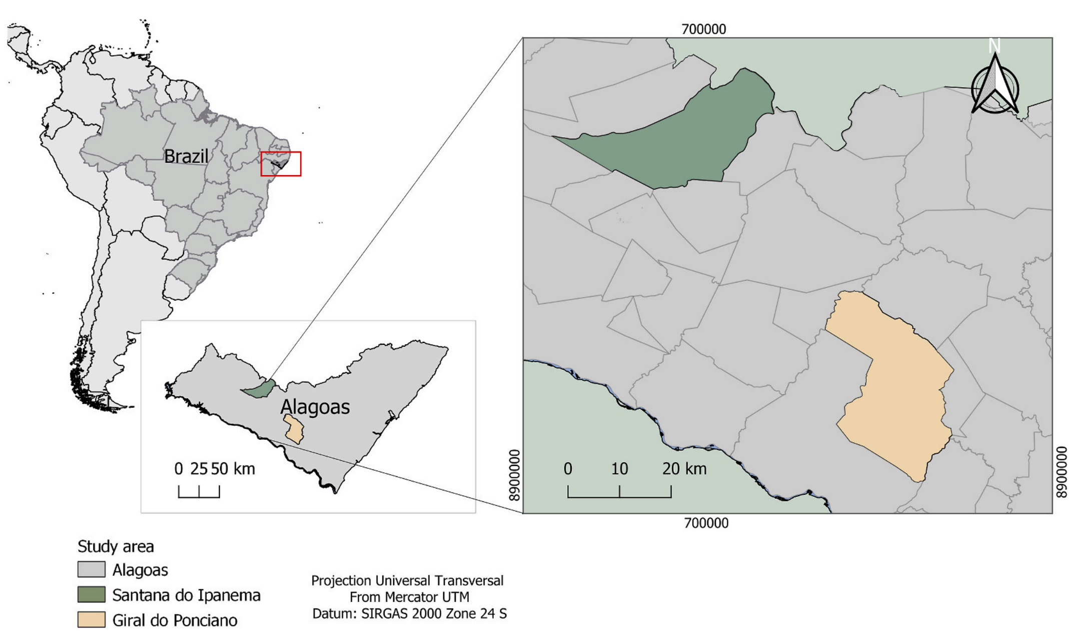

Fig. 1. Map of the location of the conserved area within the EMATER Experimental Station in the Santana do Ipanema municipality and the anthropized area in Girau do Ponciano municipality, Alagoas State, Northeastern Brazil.

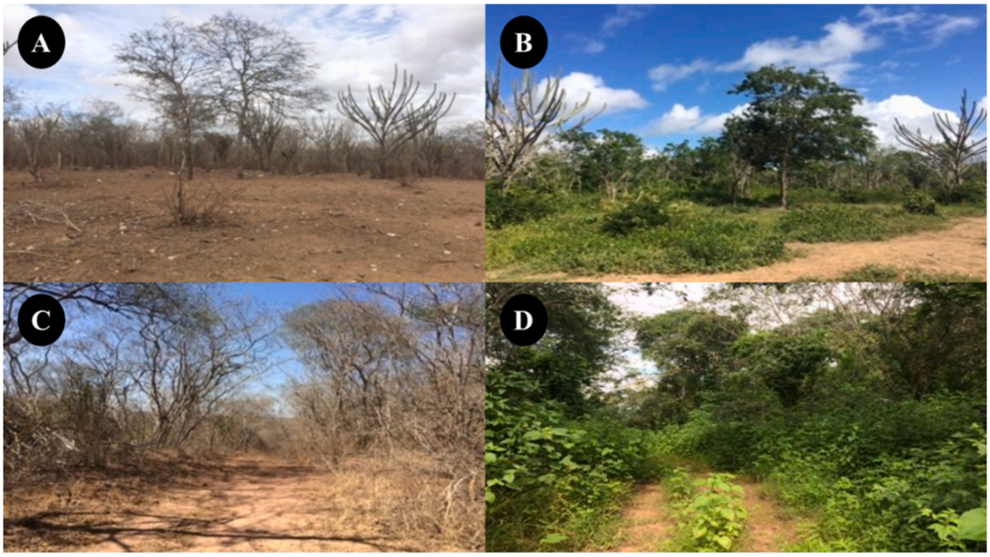

Fig. 2. Upper panels: Anthropized area (A – Dry season; B – Rainy season). Lower panels: Conserved area (C – Dry season; D – Rainy season).

2.3. Determinations of foliar N and P concentrations

The leaf samples were grounded in a knife mill (Nova Orgânica, Brazil). In total, 86 samples from each area were collected and stored in plastic containers for subsequent chemical analyses. Foliar N determination was carried out through sulfuric digestion followed by the semi-micro Kjeldahl method (Liao, 1981).

Then, 0.200g of each sample, in duplicate, was weighed on an analytical scale and placed in digestion tubes containing 2g of the catalytic digesting mixture of Na_2SO_4 and $CuSO_4$ in a ratio of 10:1. Subsequently, 5 mL of H_2SO_4 was added to each tube, and they were placed in the digestion block to slowly heat up to a temperature of 400 °C. The temperature was maintained until the solution became translucent (Silva and Queiroz, 2002; Detmann et al., 2012).

When the tubes cooled to below 100 °C, 10 mL of distilled water were added to homogenize the solution. In a 250 mL Erlenmeyer flask, 20 mL of H_3BO_3 solution (4%) were added along with three drops of a mixed solution of methyl red and bromocresol green. The Erlenmeyer flask was then connected to the N distillation assembly to receive all the distilled ammonia. Each digestion tube with the digested sample was placed in the distillation assembly, and 25 mL of NaOH (50%) were added. The total volume of the distillate was 100 mL, maintaining this value constant across all samples. Upon reaching the desired volume, the Erlenmeyer flask was removed and titrated with HCl using a 25 mL burette until the indicator color changed from green to light pink. The HCl solution used was 0.02 N, and its concentration was standardized prior to the titration step (Silva and Queiroz, 2002).

Additionally, two blank tubes (without sample) were placed in each batch, undergoing all processes (digestion, distillation, and titration) to eliminate interference and contamination from reagents and procedural parameters. All the obtained data were entered into Microsoft Excel 2010 spreadsheets to calculate N concentration, using the following formula:

$$\%NASA = \frac{(V - B)\, x\, Ne\, x\, f\, x\, 0.014\, x\, 100}{ASA}$$

Where:

$\%N_{ASA}$ = percentage of Nitrogen based on the air-dried sample;
V = volume of the hydrochloric acid solution used in titration (mL);
B = volume of hydrochloric acid used in titration of the 'blank' (mL);
Ne = expected normality of the hydrochloric acid solution;
f = correction factor of the normality of hydrochloric acid;
ASA = mass of the air-dried sample (g);
0.014 = milliequivalent-gram of Nitrogen.

The determination was performed using the Vanadate Yellow Spectrophotometry technique for foliar P concentrations. In this method, the phosphate anion (PO_4^-) reacts with molybdate (MoO_4^{2-}) and vanadate (VO_3^{2-}) in an acidic medium, forming a yellow-colored complex that absorbs light at 420 nm (Carmo et al., 2000). The equipment used was a UV–Vis Spectrophotometer (Multiskan GO, Thermo Scientific, USA). Prior to analysis, the samples were digested using 0.200 g of leaf material and placed in digestion tubes containing 4 mL of nitric acid, with 1 mL of hydrogen peroxide added after 2 h (adapted, Carmo et al., 2000).

2.4. Soil analysis

In each area, soil samples were also collected from each plot. Four individual soil samples were taken in each plot and then combined to form a composite sample. The composite samples ($n = 20$, 10 from the anthropic and 10 from the conserved area) were used for chemical attribute analysis. Soil sampling was conducted at a depth of 0–20 cm. The soil samples were air-dried in the shade, sieved, and organic materials and fine roots were removed before chemical analysis. Determination of chemical attributes was performed according to Teixeira et al. (2017) (Table 1).

2.5. Data analysis

All statistical analyses were conducted in R v. 4.3.2 using the interface RStudio v. 2023.12.1 + 402 (R Core Team, 2021). We assessed the normal distribution of the residuals (errors) with the Shapiro-Wilk test and checked for variance homogeneity with the Lavene test. Since the data did not follow a normal distribution, we applied non-parametric analysis. Kruskal and Wallis (1952) test was applied, and the Wilcoxon rank sum test (Mann-Whitney) compared the variables between areas (anthropized vs. conserved). Dunn's (1964) multiple comparisons test were performed to verify differences among botanical families within both areas. We used the base R environment for Kruskal-Wallis, Wilcoxon, and Dunn's analysis. The linear regression analysis also compared the N, P, and N/P ratio. This analysis was conducted using the "lme4" R package (Bates et al., 2015).

Table 1
Soil chemical attributes from composite samples collected in the anthropized and conserved area plots, located in the seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil.

Attributes	Anthropized	Conserved	Wilcoxon's rank sum test *p* value
pH (H_2O)	5.84 ± 0.11	5.87 ± 0.28	0.73286
Na (mg Kg^{-1})	34.50 ± 4.41	33.20 ± 2.92	0.76176
P (mg Kg^{-1})	12.50 ± 1.27	118.30 ± 17.29	0.00018
K (mg Kg^{-1})	137.70 ± 17.36	136.60 ± 14.42	0.52885
Ca + Mg ($cmol_c dm^{-3}$)	6.97 ± 0.50	11.24 ± 2.24	0.24079
Ca ($cmol_c dm^{-3}$)	4.92 ± 0.40	8.69 ± 1.67	0.07511
Mg ($cmol_c dm^{-3}$)	2.05 ± 0.17	2.55 ± 0.68	0.28773
Al ($cmol_c dm^{-3}$)	0.10 ± 0.03	0.23 ± 0.10	1.00000
H + Al ($cmol_c dm^{-3}$)	5.20 ± 0.37	5.72 ± 1.15	0.85005
C.E.C (Cation Exchange Capacity - pH 7.0)	12.71 ± 0.46	17.45 ± 1.73	0.03546
Organic Matter (dag Kg^{-1})	2.82 ± 0.18	3.68 ± 0.45	0.03409

3. Results

3.1. Species composition and soil parameters

One hundred thirty-six tree individuals were sampled in both areas: 50 in the anthropized area and 86 in the conserved area. Only 11 species were found in the anthropized area, belonging to seven families, in alphabetical order: Apocynaceae (1), Celastraceae (1), Euphorbiaceae (2), Fabaceae (4), Nyctaginaceae (1), Sapindaceae (1), and Sapotaceae (1). A higher species richness was found in the conserved site (22 species), belonging to: Anacardiaceae (3), Apocynaceae (1), Burseraceae (1), Capparaceae (1), Euphorbiaceae (2), Fabaceae (8), Myrtaceae (1), Nyctaginaceae (1), Rhamnaceae (1), Rubiaceae (1), Rutaceae (1), and Sapotaceae (1).

Soil pH ranged between 5.5 and 6.0, with an average pH of 5.84, indicating an acidic soil in the anthropized area. P concentrations ranged from 7 to 17 mg kg^{-1}, with an average of 12.5 mg kg^{-1}, and organic matter varied from 2.11 to 3.46%, with an average of 2.82% (Table 1). At the conserved area, soil pH ranged from 4.7 to 6.0, with an average of 5.87, indicating moderately acidic soil. P concentrations in the soil ranged from 44 to 184 mg kg^{-1}, with an average of 118.30 mg kg^{-1}, and the mean of organic matter was 3.68%. The Wilcoxon rank sum test showed a significant difference ($p < 0.05$) between the anthropized and the conserved areas for the variables organic matter and P contents, and the cation exchange capacity.

3.2. General patterns of foliar concentrations comparing the study areas

The concentrations of foliar N, P, and N/P were higher in plants from the conserved compared to the anthropized area (Fig. 3). In the anthropized area, foliar N concentrations ranged from 15.06 to 59.10 mg g^{-1}, with a mean of 31.55 mg g^{-1}, while foliar P concentrations ranged from 0.79 to 2.41 mg g^{-1}, with a mean value of 1.54 mg g^{-1}; the N/P ratio was 20.63 (Table 2). In the conserved site, foliar N showed greater variation, ranging from 26.24 to 83.34 mg g^{-1}, with a mean of 49.25 mg g^{-1} while foliar P concentrations ranged from 0.91 to 7.13 mg g^{-1}, with a mean of 2.22 mg g^{-1}, and the N/P ratio was 26.54.

3.3. General patterns of foliar concentrations across families

Differences in foliar concentrations were observed for plant families (26 spp. found) considering Fabaceae and non-Fabaceae. N-fixing Fabaceae (F+) showed a wide variation in foliar concentration values in the conserved area but there was no statistical difference in comparison to the anthropized site (Fig. 4). However, the F+ group stood out with higher averages of 56.50 mg g^{-1} for foliar N (Figs. 4A) and 2.84 mg g^{-1} for foliar P concentrations (Fig. 4B). The non-fixing Fabaceae (F-) and non-Fabaceae (non-fixing, NF) groups tended to show higher foliar concentrations of N, P and the N/P ratio in the conserved area. The F- group also showed high P content, with an average of 1.97 mg g^{-1}, and the N/P ratio was high for both NF and F+ groups, with values ≥ 20 (Fig. 4C).

In both areas, the families with the highest foliar N concentrations

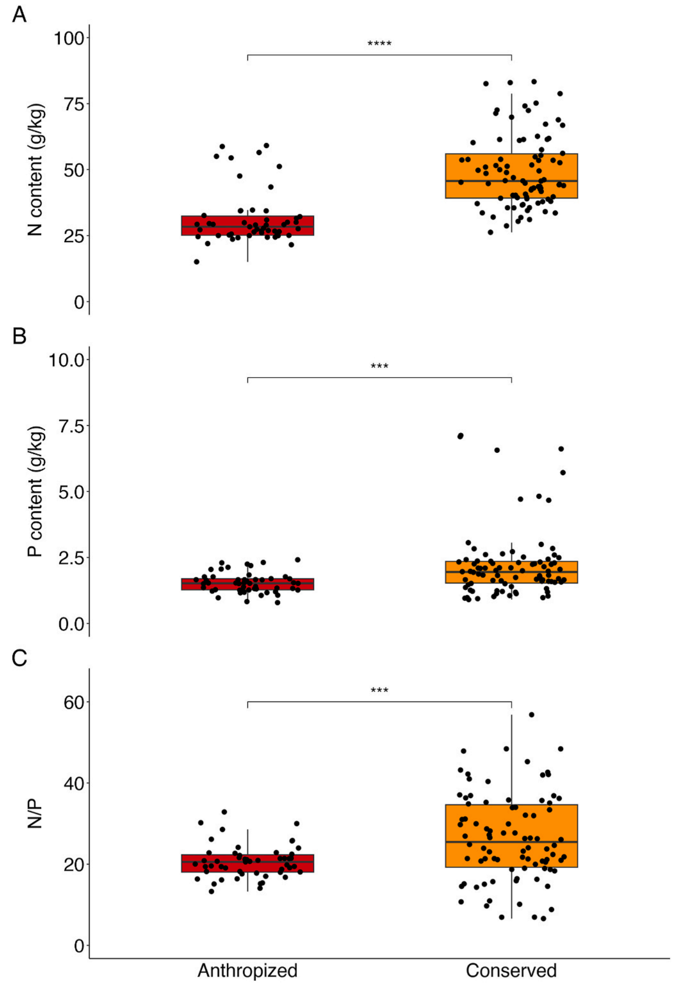

Fig. 3. Foliar nitrogen (A) and phosphorus (B) concentrations, and N/P ratio (C), of tree species from anthropized and conserved areas in the seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil. Symbols indicate significant differences by the Wilcoxon's rank sum test (Mann-Whitney) (**** = $p < 0.0001$, *** = $p < 0.001$).

Table 2
General characteristics of foliar N and P stoichiometry for the 26 species studied within the anthropized and conserved areas located in the seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil (mean ± standard deviation, n = 86). CV = coefficient of variation; SE = standard error.

	Anthropized			Conserved		
	N (mg g^{-1})	P (mg g^{-1})	N/P	N (mg g^{-1})	P (mg g^{-1})	N/P
Mean	31.55	1.54	20.63	49.25	2.22	26.54
Minimum	15.06	0.79	13.29	26.24	0.91	6.61
Maximum	59.10	2.41	32.87	83.34	7.13	56.83
CV (%)	10.29	0.38	4.12	13.67	1.33	10.82
SE	1.47	0.05	0.59	1.48	0.14	1.17

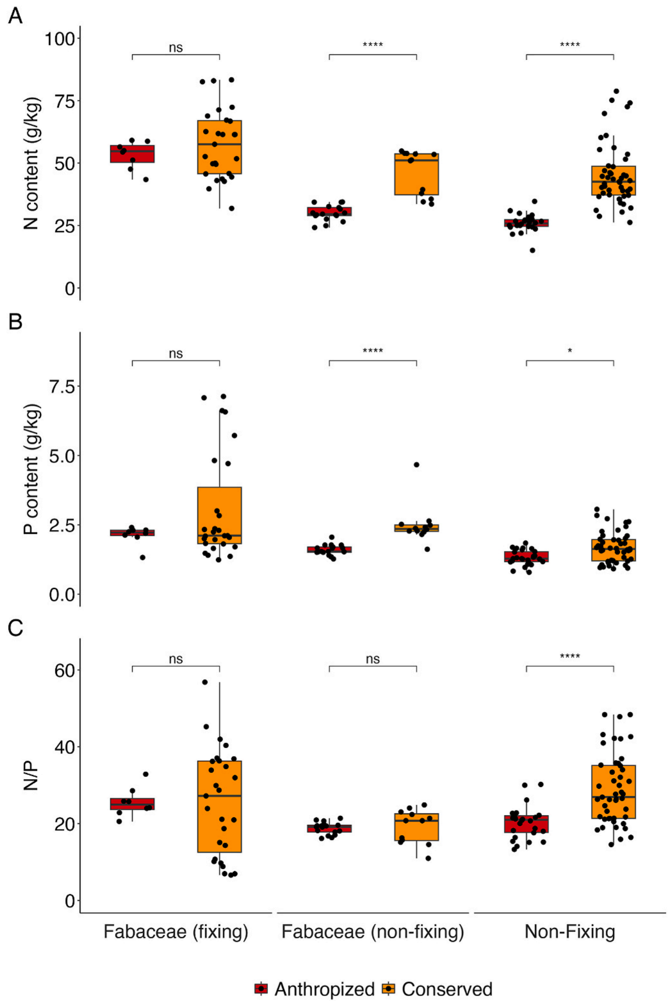

Fig. 4. General comparison of leaf nitrogen (A), phosphorus (B) concentrations, and N/P ratio (C), of each group: fixing Fabaceae, non-fixing Fabaceae, and non-Fabaceae (non-fixing) from seasonally tropical dry forest (Caatinga) in the semiarid region of Northeast Brazil. Symbols indicate significant differences between them by the Wilcoxon's rank sum test (Mann-Whitney) (**** = $p < 0.0001$, *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = $p > 0.05$).

were Rutaceae, Nyctaginaceae, Rubiaceae, Fabaceae, Rhamnaceae, Burseraceae, Anacardiaceae, Capparaceae, Myrtaceae, and Sapotaceae (Table 3). The families that stood out for foliar P concentrations were Rubiaceae, Nyctaginaceae, Fabaceae, Burseraceae, and Rutaceae. The families with the highest averages for the N/P ratio were Anacardiaceae, Rutaceae, Capparaceae, Myrtaceae, Nyctaginaceae, Sapotaceae, Rhamnaceae, and Burseraceae.

Table 3
Overview of foliar N and P contents, and N/P ratio, from tree families from seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil.

Plant families	*n*	N (mg g^{-1})	P (mg g^{-1})	N/P
Anacardiaceae	4	41.40 ± 1.43^{abc}	1.07 ± 0.07^{c}	38.39 ± 2.35^{a}
Apocynaceae	17	32.04 ± 1.70^{bc}	1.57 ± 0.11^{bc}	20.86 ± 0.73^{bc}
Burseraceae	3	42.40 ± 5.36^{abc}	1.80 ± 0.15^{abc}	24.10 ± 1.77^{abc}
Capparaceae	7	40.12 ± 2.58^{abc}	1.03 ± 0.04^{c}	39.24 ± 3.19^{ab}
Euphorbiaceae	16	29.60 ± 2.12^{c}	1.56 ± 0.06^{bc}	18.93 ± 0.90^{c}
Fabaceae	64	47.49 ± 1.91^{ab}	2.45 ± 0.18^{ab}	22.58 ± 1.23^{bc}
Myrtaceae	4	36.08 ± 3.51^{abc}	1.18 ± 0.07^{bc}	30.41 ± 2.15^{abc}
Nyctaginaceae	4	64.14 ± 11.36^{a}	2.13 ± 0.36^{ab}	30.0 ± 2.56^{abc}
Rhamnaceae	4	44.57 ± 6.97^{abc}	1.50 ± 0.10^{bc}	29.74 ± 4.10^{abc}
Rubiaceae	5	49.70 ± 3.36^{ab}	2.56 ± 0.23^{a}	19.58 ± 0.64^{bc}
Rutaceae	3	69.61 ± 6.58^{a}	1.74 ± 0.12^{abc}	40.49 ± 6.22^{ab}
Sapotaceae	4	35.02 ± 7.12^{abc}	1.25 ± 0.29^{bc}	28.61 ± 1.03^{abc}

Note: Different lowercase letters indicate significant differences ($P < 0.05$) by Dunn's Test in the concentrations of foliar N, P, or N/P within each family.

3.4. Linear regression analysis among foliar N, P, and N/P

The regression analysis among foliar N, P, and N/P ratios showed significant trends among the 26 species. Foliar concentrations of N and P exhibited a significant allometric relationship (Fig. 5A), indicating that as foliar P increases, foliar N also increases. Similarly, the foliar N/P ratio also showed a growing allometric trend with increasing foliar N (Fig. 5B). With an increase in foliar P, the N/P ratio decreases (Fig. 5C).

3.5. Foliar concentrations for the main species in each area

The species that stood out for foliar N concentrations in the anthropized area were *Mimosa ophthalmocentra* and *Bauhinia forficata*, representing Fabaceae (Table 4). The highest foliar P concentrations were also found in *M. ophthalmocentra* and *B. forficata* (F+ and F-, respectively). Regarding N/P, most species in the anthropized area exhibited relatively high ratios, except for *Croton blanchetianus* (Euphorbiaceae), which showed the lowest value.

In the conserved area, *G. opposita* (Nyctaginaceae) had the highest N concentration, followed by *Dictyoloma vandellianum* (Rutaceae), *M. ophthalmocentra and Senegalia bahiensis* (Fabaceae). Within this site, most species showed high foliar N concentrations (>40 mg g^{-1}, Table 5), except for *Aspidosperma pyrifolium* (Apocynaceae), and *Eugenia pyriformis* (Myrtaceae). The species with higher P concentrations were mostly Fabaceae: *Anadenanthera colubrina*, *Anadenanthera falcata*, *B. forficata*, but *Coutarea hexandra* (Rubiaceae) and *G. opposita* also stood out.

In relation to the species commonly occurring in both areas, it was observed that *A. pyrifolium* (NF), *B. forficata* (F-), and *M. ophthalmocentra* (F+) showed higher concentrations of leaf N in the conserved site (Fig. 6A). For leaf P, *A. pyrifolium* and *B. forficata* also showed higher P concentrations in the conserved area (Fig. 6B). *Mimosa ophthalmocentra* showed no variation in P between the two areas but presented a high N/P ratio in the conserved site (Fig. 6C).

4. Discussion

4.1. Environmental effects on foliar and soil stoichiometry

The arboreal species found in both areas differed in foliar content characteristics of N, P, and the N/P ratio. These responses provide new insights into plant adaptation mechanisms to environmental changes and anthropogenic action in determining foliar stoichiometry in seasonally dry tropical forests. In the conserved site, the greater species richness may be attributed to more efficient nutrient cycling, as evidenced by the increased N and P concentrations in leaves. According to Silva et al. (2021), differences in litter decomposition among forest species in species-rich Caatinga areas allow for continuous nutrient cycling; when the litter of one group of species ceases decomposition, other groups assume this role, maintaining the cycle.

The Caatinga has been rapidly deforested, mainly due to agricultural use, extensive livestock farming, and timber extraction (Ribeiro et al., 2015), resulting in reductions of biomass stock and production, which decreases litter deposition and compromises nutrient cycling (Souza et al., 2017). As the study was conducted at the beginning of the dry season, soil in both regions was still relatively moist despite the high temperatures. Climatic variables such as light intensity, mean annual temperature, and mean annual precipitation partially determine nutrient absorption in plants and, therefore, foliar elemental concentrations and stoichiometry (Tong et al., 2020; Lin et al., 2022; Wang et al., 2023). However, these factors are also influenced by other ecosystem resources, including dominant plant growth strategies,

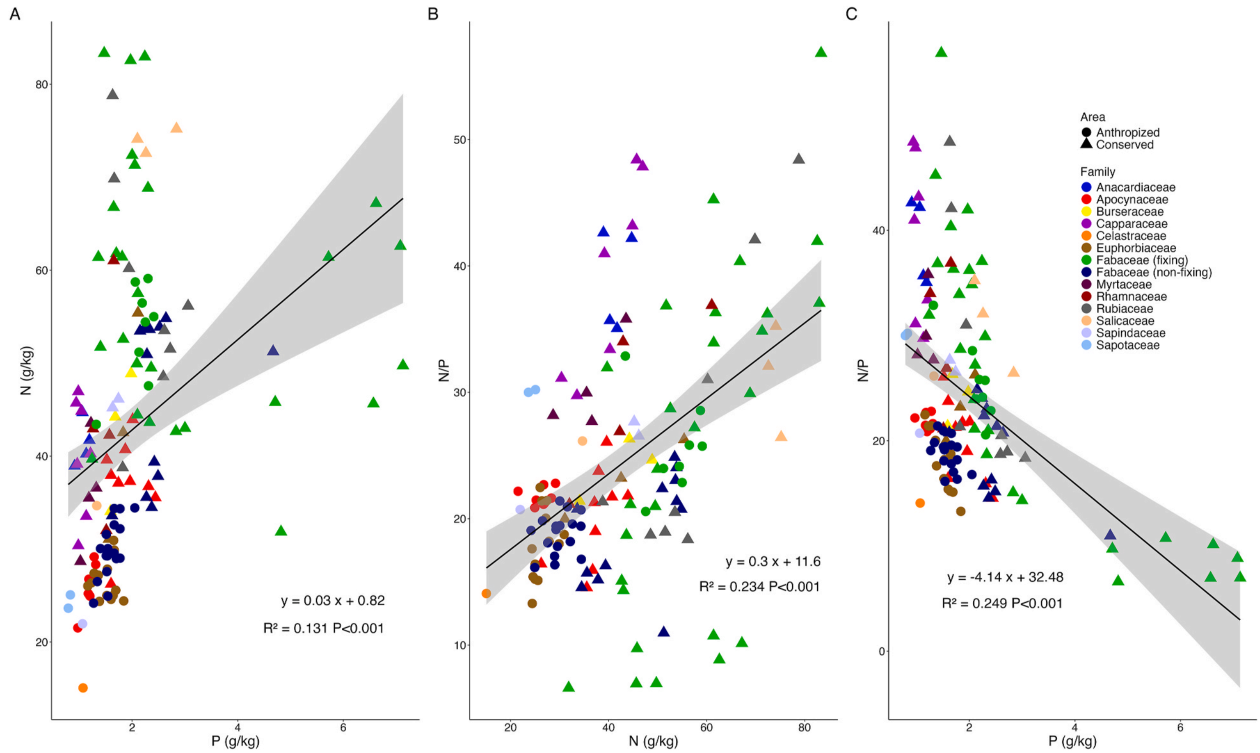

Fig. 5. Linear regressions between foliar N and P concentrations, and foliar N/P ratios, of 26 tree species in seasonally tropical dry forest (Caatinga) areas of Northeast Brazil. Linear equations, R^2, and p values are shown in each plot.

Table 4
Foliar stoichiometry of N and P for the main species within the anthropized area, located in the seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil.

Main species in Anthropized area	Family	*n*	N (mg g^{-1})	P (mg g^{-1})	N/P
Aspidosperma pyrifolium	Apo	8	26.19 ± 0.89^{b}	1.2 ± 0.04^{c}	21.75 ± 0.27^{ab}
Bauhinia forficata	Fab	7	32.33 ± 0.91^{ab}	1.70 ± 0.07^{ab}	19.13 ± 0.67^{ab}
Croton blanchetianus	Eup	10	25.84 ± 0.56^{b}	1.51 ± 0.07^{b}	17.50 ± 0.10^{b}
Jatropha molissima	Eup	3	28.72 ± 1.36^{b}	1.48 ± 0.134^{bc}	19.46 ± 1.22^{ab}
Mimosa ophthalmocentra	Fab	7	54.64 ± 1.68^{a}	2.23 ± 0.05^{a}	24.52 ± 1.03^{ab}
Poincianella pyramidalis	Fab	10	28.25 ± 0.82^{b}	1.5 ± 0.06^{b}	18.54 ± 0.53^{ab}

Note: Different lowercase letters indicate significant differences ($P < 0.05$) by the Dunn's Test on the foliar concentrations of N, P, or N/P within each group. Apo: Apocynaceae. Eup: Euphorbiaceae. Fab: Fabaceae.

community composition, and soil nutrient heterogeneity (Sardans et al., 2016; Wang et al., 2016; Chang et al., 2022), as observed in both study sites.

The concentrations of organic matter and P were lower in the soil of the anthropized area, suggesting that such patterns result from human interventions in this area, which entail considerable nutrient losses (Holanda et al., 2017). Due to the close relationship between soil and plant nutritional status, soil use changes affect plant nutrient concentrations and plant stoichiometric characteristics (Tao et al., 2019; Chang et al., 2022). In contrast, the highest concentration of P in the conserved Caatinga's soils contributed to the increase in P and N in the leaves. Soil P is generally considered the main determinant for N and P assimilation by roots and translocation to the leaves (Liu et al., 2019). Soil P originates from rock weathering and, after being absorbed by plants, is

Table 5
Foliar stoichiometry of N and P for the main species within the conserved area, located in the seasonally dry tropical forest (Caatinga) in the semiarid region of Northeast Brazil.

Main species in Conserved area	Family	*n*	N (mg g^{-1})	P (mg g^{-1})	N/P
Aspidosperma pyrifolium	Apo	9	37.23 ± 1.71^{c}	1.89 ± 0.11^{bc}	20.06 ± 1.36^{ab}
Anadenanthera colubrina	Fab	7	52.03 ± 5.06^{abc}	6.09 ± 0.42^{a}	8.57 ± 0.70^{b}
Anadenanthera falcata	Fab	4	45.47 ± 2.75^{abc}	2.50 ± 0.30^{ab}	19.20 ± 3.81^{ab}
Bauhinia forficata	Fab	10	46.79 ± 2.91^{abc}	2.37 ± 0.05^{ab}	19.82 ± 1.32^{ab}
Cynophalla flexuosa	Cap	7	40.12 ± 2.58^{bc}	1.03 ± 0.04^{d}	39.24 ± 3.19^{a}
Coutarea hexandra	Rub	5	49.70 ± 3.36^{abc}	2.56 ± 0.228^{ab}	19.57 ± 0.64^{ab}
Commiphora leptophloeos	Bur	3	42.39 ± 5.36^{abc}	1.75 ± 0.14^{bcd}	24.12 ± 1.77^{a}
Dictyoloma vandellianum	Rut	3	69.61 ± 6.58^{ab}	1.74 ± 0.12^{bcd}	40.49 ± 6.22^{a}
Eugenia pyriformis	Myr	4	36.08 ± 3.51^{c}	1.18 ± 0.07^{d}	30.41 ± 2.15^{a}
Guapira opposita	Nyc	3	73.97 ± 0.93^{a}	2.40 ± 0.27^{ab}	31.24 ± 3.15^{a}
Mimosa ophthalmocentra	Fab	5	67.51 ± 4.86^{ab}	2.02 ± 0.14^{bc}	33.69 ± 2.65^{a}
Senegalia bahiensis	Fab	7	64.78 ± 6.72^{ab}	2.00 ± 0.11^{bc}	33.70 ± 5.34^{a}
Parapiptadenia zehntneri	Fab	4	53.66 ± 6.00^{abc}	1.43 ± 0.11^{cd}	37.59 ± 3.21^{a}
Ziziphu sjoazeiro	Rha	4	44.56 ± 8.53^{abc}	1.50 ± 0.12^{cd}	29.74 ± 5.02^{a}

Note: Different lowercase letters indicate significant differences ($P < 0.05$) by the Dunn's Test in the concentrations of N, P, or N/P foliar of each group. Apo: Apocynaceae. Bur: Burseraceae. Cap: Capparaceae. Fab: Fabaceae. Myr: Myrtaceae. Nyc: Nyctaginaceae. Rha: Rhamnaceae. Rub: Rubiaceae. Rut: Rutaceae.

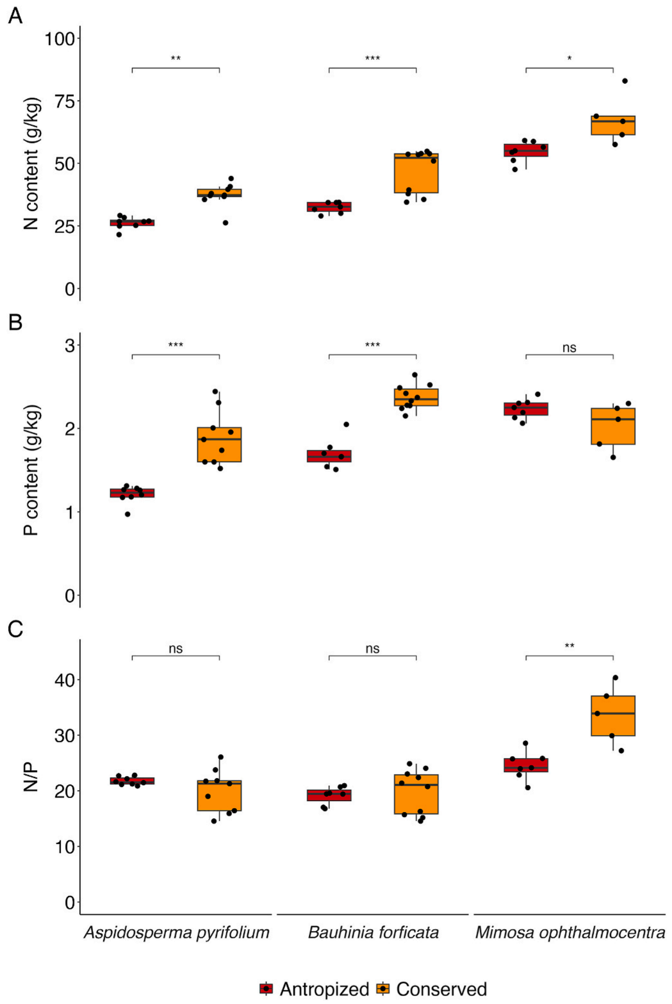

Fig. 6. Foliar concentrations of N, P, and N/P ratio for *Aspidosperma pyrifolium*, *Bauhinia forficata*, and *Mimosa ophthalmocentra* in the anthropized and conserved areas, located in the seasonally tropical dry forest (Caatinga) in the semiarid region of Northeast Brazil. Symbols indicate significant differences between them by the Wilcoxon's rank sum test (Mann-Whitney) (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = $p > 0.05$).

returned to the soil through litter production and decomposition (Wang et al., 2023). The higher concentrations of N and P in the leaves (and P in the soil) at the conserved site might also be related to the better quality of litter due to the greater diversity of tree species in the region, which enhances decomposition and increases nutrient availability in this ecosystem (Wang et al., 2016; Silva et al., 2021).

Plants in the conserved site showed a higher N/P ratio in their leaves, which can be attributed to the high concentrations of P in the soil at that location. Nitrogen deposition promotes plant absorption of soil P by increasing root phosphatase activity or stimulating the plant to use the remaining N to produce this enzyme (Yu et al., 2018; Chang et al., 2022). This is in line with the biogeochemical hypothesis, which emphasizes the crucial role of soil nutrient availability in determining leaf nutrient content (Hu et al., 2021).

In foliar stoichiometry studies with tree species from Chinese fir forests, leaf N and P concentrations were mainly driven by longitude and total soil P content, which is also consistent with the prediction of the biogeochemical hypothesis (Chang et al., 2022). Another study conducted in a tropical forest with conifer species of the Cupressaceae family found that leaf P concentration and N/P ratio increased exponentially with soil P concentration (Tong et al., 2020). Zhang et al. (2022), investigating leaf and twig stoichiometry in a primary karst forest plant community in China, found that the highest nutrient use efficiencies of C, N, and P were in the leaves and were closely related to altitude, soil pH, and total soil P.

Overall, when analyzing all 26 species from the study together, they exhibited an allometric relationship; as leaf N increased, the leaf N/P ratio also increased (see Fig. 5B). Conversely, a low N/P ratio in the anthropized area indicates that plant growth may be limited by N availability (Tong et al., 2020; Wang et al., 2023). Thus, leaf N/P ratio was an effective method for assessing plant health and growth and understanding the plants' adaptability to environment and stress (Sardans et al., 2016; Zhang et al., 2022).

In addition, increased leaf P led to a decreased N/P ratio (Fig. 5C). This may be related to the higher availability of P in the soil, as the analyses were conducted at the transition between the end of the rainy season and the beginning of the dry season. Consequently, soils were still moist and rich in organic matter, especially in the conserved Caatinga. This suggests that the leaf N/P ratio is influenced by land use and seasonal factors in the Caatinga. Wang et al. (2023) found that in a study of leaf samples from 268 species across four locations in warm and humid tropical forests on Hainan Island, China, leaf P concentration increased while C/P and N/P ratios decreased with rising rainfall. This indicates that the leaf N/P ratio varies with geographical and climatic factors. Liu et al. (2021) noted that soil properties had a greater impact than climatic factors on N/P stoichiometric variations in Qinghai spruce (*Picea crassifolia*) forests in the Qilian Mountains, China.

4.2. Patterns of foliar concentrations across families

Fabaceae was the most representative family regarding species number in both study areas, reflecting its high species richness in the Caatinga (Fernandes et al., 2020). Notably, fixing Fabaceae (F+) were more prominent in leaf N and P stoichiometry, underscoring their role in nutrient cycling. This advantage is likely due to their biological nitrogen fixation system (Dias et al., 2020). In a study of leaf stoichiometry of herbs, shrubs, and trees in China, the Fabaceae family had the highest concentrations of leaf N and P among the many families studied (Tao et al., 2016). The high concentrations of these nutrients were linked to the efficiency of rhizobia in N uptake by Fabaceae nodules.

Silva et al. (2021) found that Fabaceae species showed different groups with shared decomposition rates in their study of C and N release from litter in the Caatinga. This suggests that nutrient cycling among Fabaceae species is crucial for preserving the Caatinga. Besides Fabaceae, the Rutaceae, Nyctaginaceae, Rubiaceae, and Burseraceae families also exhibited high concentrations of N and P in both Caatinga areas, suggesting a possible synergistic relationship between N and P absorption efficiency in these plants, highlighting their efficient nutritional strategies as an adaptive mechanism to the semiarid environment.

Fixing Fabaceae and Nyctaginaceae species had the highest leaf N concentrations in anthropized sites, while F+ and F- exhibited elevated leaf P concentrations. Therefore, using Fabaceae species is a viable strategy for recovering anthropogenically degraded areas in the Caatinga, as they accumulate significant amounts of leaf N and P (Carvalho et al., 2022). This accumulation allows the soil to retain and cycle these nutrients through the degradation of plant biomass, thereby aiding in the conservation of various ecosystems (Souza et al., 2019).

In contrast, the conserved Caatinga site exhibited a greater diversity of families with high N/P ratios, including Rutaceae, Anacardiaceae, Capparaceae, Fabaceae, Nyctaginaceae, Myrtaceae, Rhamnaceae, among others. This indicates that species diversity in the Caatinga results in varied nutrient acquisition strategies, leading to an efficient N/P ratio in most species within a conserved environment. In Caatinga forests, the tree component plays a significant role in nutrient cycling through litter production from diverse species (Souza et al., 2017; Souza et al., 2019; Carvalho et al., 2022). This process is crucial for the return of elements through soil-plant nutrient cycling. Thus, this study highlights that variations in the stoichiometric characteristics of tree species in seasonally dry forests are influenced not only by environmental conditions but primarily by species diversity.

4.3. Foliar concentrations of the main study species

Taxonomic impoverishment was observed at the anthropized site, changing the plant community structure in this area. Nevertheless, some species were resilient, demonstrating a higher capacity for N and P assimilation and nutrient storage. Species such as *M. ophthalmocentra* and *M. tenuiflora*, both F+, in addition to *B. forficata* (F-), and *G. opposita*, from Nyctaginaceae, presented high concentrations of leaf N. The highest concentrations of leaf P were found in *M. ophthalmocentra* and *B. forficata*. These findings indicate these species as efficient nutrient users under environmental degradation by human activities conditions, making these species suitable candidates for restoration efforts in the Brazilian drylands.

In the conserved site, most species exhibited high concentrations of leaf N, with the exceptions of *S. brasiliensis* (Euphorbiaceae) and *A. pyrifolium* (Apocynaceae). Silva et al. (2021), studying the decomposition of litter from Caatinga plants, found that *A. pyrifolium*, despite being well-adapted to the semiarid region, showed low nutrient decomposition and reduced N concentrations due to its non-N-fixing nature. Most species with higher concentrations of leaf P in this site belonged to Fabaceae, with *A. colubrina* standing out with a high leaf P content compared to the other legume species. Such high P concentrations can be explained by the species' broad adaptation to various climatic and environmental conditions, favoring a greater efficiency in nutrient cycling. It is important to highlight that N-fixing legumes can be associated more efficiently with soil mycorrhiza than the non-fixing species (Sanginga et al., 1995; Toro et al., 2023), increasing the plant P uptake and translocation to the leaves. Probably, for this reason, we observed higher P concentrations in the leaves of the N-fixing species than in the non-fixing legumes.

For the main species occurring in both areas, *A. pyrifolium* (Apocynaceae) and *B. forficata* (F-), had higher concentrations of foliar P and N in the conserved area rather than in the anthropized one. These findings demonstrates that in a well-conserved environment, better soil nutrient conditions due to higher litter decomposition, positively influence the nutritional strategies of these plants. *Mimosa ophthalmocentra* showed a high N/P ratio in both areas compared to the other species. This may result from enhanced nutrient uptake capabilities, as this species is a fixing Fabaceae (Dias et al., 2020), also presenting effective adaptation to dry environmental conditions. This species thrives in anthropized areas and shows a broad tolerance to different soil physicochemical parameters (Silva et al., 2011).

Plant species with different life forms generally exhibit different leaf stoichiometry according to geographical and climatic variations, reflecting diverse strategies for utilizing C, N, and P (Chang et al., 2022; Lin et al., 2022). Research on tropical forest species has shown that leaf N and P stoichiometry can be affected by temperature (Tong et al., 2020), precipitation (Lin et al., 2022; Wang et al., 2023), and soil nutrients (Chang et al., 2022). The present study found that ecosystem degradation contributed to soil nutrient impoverishment, resulting in plants with lower foliar nutrient concentrations. These findings support and encourage further stoichiometric studies in the Caatinga ecosystem to explore variations in foliar nutrient concentrations in greater depth and to better understand species' responses to anthropogenic changes.

5. Conclusion

Nutrient cycling occurs more efficiently in the well-conserved site, where species richness enhances nutrient production in the soil, leading to higher concentrations of leaf N and P compared to the anthropized area. The lower leaf N/P ratios observed in the anthropized forest indicate that, from a nutritional point of view, anthropogenic impacts reduce species richness and nutrient availability in seasonally dry tropical forests, affecting the Caatinga's regeneration capacity. Tree species from fixing Fabaceae showed resilience in both conserved and anthropized areas, with efficient absorption of leaf N and P. These results are crucial for developing plant growth models, enhancing the understanding of nutrient cycling, and improving predictions about how forest degradation and reduced forest cover may impact nutrient cycling in global contexts of progressive land degradation.

CRediT authorship contribution statement

Elizabete Cristina Araújo Silva: Writing – review & editing, Writing – original draft, Visualization, Validation. **Jakson Leite:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation. **Maria Claudjane Jerônimo Leite Alves:** Writing – original draft, Visualization, Validation. **Claudiana Moura dos Santos:** Writing – review & editing. **Luís Felipe Daibes:** Writing – review & editing. **Paulo Ivan Fernandes-Júnior:** Methodology, Formal analysis, Data curation. **Flávia de Barros Prado Moura:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **José Vieira Silva:** Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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