



Article

Potentially Toxic Cyanobacteria in a Eutrophic Reservoir in Northern Colombia

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Abstract: The El Guájaro reservoir, situated in northern Colombia, holds significant economic and ecological importance. It is categorized as eutrophic due to factors such as wastewater discharges, agricultural practices, and the dragging of limestone material. These factors create favorable conditions for cyanobacterial proliferation. This study evaluates the diversity and abundance of cyanobacteria, with special attention to the genera identified as toxin producers, and bloom formers within the reservoir. Sampling was conducted in the photic zone at seven stations during both rainy and dry seasons between 2015 and 2019. Abundance and diversity were quantified using the iNEXT program, while a beta diversity analysis assessed community differentiation in relation to environmental parameters. A total of 86 species from 12 orders and 42 genera were identified, with 44% of these species noted as potentially toxic. A significant predominance of filamentous species was identified. *Pseudanabaena* and *Phormidium* were the most frequent and abundant genera. The results reveal distinct distribution and abundance patterns influenced by seasonal fluctuations. A notable bloom, co-dominated by *Microcystis* and *Dolichospermum*, occurred during the 2019 dry season, leading to the mortality of livestock and other animals. Urgent governance measures and control strategies are imperative to mitigate the health impact of such blooms.

Keywords: planktonic cyanobacteria; El Guájaro reservoir; diversity; abundance; Colombia; eutrophic reservoir



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1. Introduction

Presently, the factors that contribute to the proliferation of harmful cyanobacteria in aquatic ecosystems are broadening. This expansion is related to the increase of nutrients, the dissemination of strains through anthropogenic activity, the burgeoning expansion of aquaculture production, and even overfishing, which disrupts food webs. This disruption enables harmful species to dominate within the phytoplankton community [1].

Suboptimal light conditions and temperature fluctuations trigger a series of reactions that significantly impact cyanobacteria physiology [2]. Climate change and eutrophication are amplifying eco-physiological processes that trigger cyanotoxin production, leading to heightened cyanobacterial proliferation and elevated cyanotoxin levels. These conditions are expected to persist, extend, and worsen in the future [3].

The physiological plasticity of cyanobacteria is consistent with their long evolutionary history, which has allowed them to thrive in both extreme and rapidly changing environments. However, being such a heterogeneous group, represented by more than 3000 species with different adaptive capacities, the correlation with the factors that promote these blooms are still debatable. Some studies indicate that toxic genotypes of cyanobacteria are advantaged over non-toxic ones [4]. Genera such as *Microcystis*, *Oscillatoria*, *Planktothrix*, *Radiocystis*, *Dolichospermum*, *Cylindrospermopsis*, and *Nostoc* are mainly related to the formation of blooms and the production of cyanotoxins [5].

Bloom-forming cyanobacterial species, often initiate competitive processes and ecological successions between diazotrophic and non-nitrogen-fixing species [6,7]. However, contrary theories have been proposed, such as the induction of allelopathic events in toxic species that suppress the presence of other cyanobacteria [8–11]. This demonstrates the complexity of biotic interactions, making it challenging to comprehend the mechanisms through which environmental factors regulate the pattern of cyanobacterial bloom formation and cyanotoxin production [12].

In eutrophic and hypertrophic lakes, the occurrence of blooms may be associated with spatiotemporal patterns of nutrient distribution [13,14] or with specific climatic conditions that promote their proliferation. In this context, there is a need to improve the capability to detect and monitor the factors that trigger the formation of cyanobacterial blooms. It is crucial to implement specific strategies in aquatic systems to mitigate the impacts of both climate change and eutrophication. This necessitates a thorough understanding of the dynamics of cyanobacterial communities within these systems, the identification of the potential parameters responsible for toxin production, and the effective communication of these risks to the population [1,15,16].

Our study aims to investigate the relationship between physicochemical variables, and the abundance and dominance of cyanobacteria in the El Guájaro reservoir. This system holds significant importance in northern Colombia and has been designated as a strategic ecoregion. It is recognized as the second most important reservoir in the country due to its extension and remarkable productivity, as affirmed by the FAO [17,18].

We primarily investigated the genera that showed a significant presence in the reservoir, and that have been documented as both toxin producers and bloom formers. This analysis provided insights into their behavior within the system over a five-year period.

Considering the fundamental role of this reservoir in the local economy and its importance in meeting the water needs of nearby communities, acquiring a detailed knowledge of the cyanobacterial populations is crucial. This knowledge is essential to formulate clear objectives to improve reservoir management.

2. Materials and Methods

2.1. Description of the Study Area

The El Guájaro reservoir is located in northwestern Colombia, south of the Atlántico department, at coordinates 10°30'36" N, 75°1'48" W. Its creation resulted from the artificial merging of several swamps and was constructed between 1964 and 1965. Presently, it spans an expansive area of 12,200 ha with a total volume of 400 Mm³. It boasts an average depth of 5 m and a utilizable volume of 230 Mm³ [17].

The reservoir is supplied by two floodgates systems: El Limón and Villa Rosa. Both are interconnected with the Dique canal, a branch stemming from the Magdalena River [17]. The hydrographic basin of the reservoir covers a total area of 921 km² and is subdivided into 31 sub-basins that ultimately converge in the Dique canal.

Currently, the floodgates are operated following a protocol that outlines specific opening and closing procedures, considering the hydrological conditions and water levels in both the reservoir and the Dique canal. However, the efficient execution of this protocol faces obstacles due to problems arising from its misuse by residents, who frequently manipulate the floodgates according to their needs, disregarding the established guidelines [17,19,20].

This system is considered one of the largest and most important bodies of water in the region. The El Guájaro reservoir serves as a crucial fish reserve, supports extensive agricultural activities, aquaculture, and livestock maintenance, and serves as a drinking water supply [19]. Until 2004, the reservoir covered a surface area of 16,000 ha; however, a series of stress factors has led to a reduction in the water body. The inadequate use given to the areas of influence has generated high sedimentation, mainly from the Dique canal, the discharge of domestic wastewater from neighboring municipalities, and contamination with fecal bacteria. Additionally, the inflow of heavy metals, pesticides, and fertilizer runoff

due to inadequate agricultural practices, along with deforestation on nearby hillsides, has aggravated eutrophication [19–23].

The Autonomous Regional Corporation (CRA) functions as the environmental authority responsible for monitoring the management and water quality of the reservoir; according to analyses of phosphorus, nitrogen, and chlorophyll data, this system has been categorized as eutrophic [20,21,23–27]. Due to its geographical location, the climate of this area is dry tropical, and the water body is exposed to intense levels of solar radiation [19,24].

The reservoir experiences seasonal fluctuations characterized by alternating periods of precipitation and drought, with typical annual temperatures ranging between 28 °C and 29 °C. The dry season spans from December to April, succeeded by an intermediate period with reduced rainfall extending from May to early September. October and November are characterized by the highest temperatures and peak levels of precipitation [24]. Additionally, this region experiences a heightened evaporation rate, averaging around 1500 mm annually. Noteworthy is the escalating variability between dry and rainy periods in the area, attributable to anomalies arising from the climatic phenomena of El Niño and La Niña [17–19,24].

2.2. Sampling and Analysis

The samples were collected between 2015 and 2019, averaging four expeditions per year, conducted between 7:00 and 12:00 am. The study spans the dry and rainy seasons. However, the climatic conditions in 2015 and 2019 were recorded as anomalous, with rainfall deficit in much of the Colombian Caribbean region, with reductions of up to 75% [28,29].

Seven sampling sites were selected and distributed between the northern, central, and southern zones of the reservoir, including the fish farm of the National Aquaculture and Fisheries Authority, where different fish species are cultivated for restocking in the reservoir (Figure 1; Table 1). In each sector, the parameters of temperature (T), electrical conductivity of water, pH, and dissolved oxygen (DO) were measured using a multiparameter probe YSI 6600 V2, previously calibrated according to technical recommendations. For the measurement, the 5-day biochemical oxygen demand (BOD5) test and the total suspended solids (TSS) test were used, following the protocol established in the 21st edition of Standard Methods.

Table 1. Location and description of the stations studied in the El Guájaro reservoir (2015–2019).

Station Code	Location	Coordinates	Description
North zone			
LP	La Peña	10°35′19″ N 75°01′53″ W	Area adjacent to the town of La Peña, with fish farming, shrimp farming, and domestic sewage.
Central zone			
RO	Rotinet	10°31′33″ N 75°04′56″ W	Area adjacent to the town of Rotinet-Repelón, with high impact due to limestone mining, agriculture and livestock.
RE	Repelón	10°29′01″ N 75°06′38″ W	Zone close to fish farming in an area of approximately 500 ha, livestock, artisanal fishing and rice, banana and citrus crops.
AC	Aqueduct system of the Repelón área	10°30′59″ N 75°05′29″ W	Catchment and aqueduct for human consumption.
EP	Aquaculture station	10°31′20″ N 75°05′59″ W	Fish station reservoir of the National Aquaculture and Fisheries Authority.
South zone			
LC	Floodgates El Limón	10°25′37″ N 75°04′06″ W	System of four radial gates with a capacity of up to 250 m ³ /s. Area with high content of suspended solids and organic matter.
VR	Floodgates Villa Rosa	10°25′20″ N 75°06′47″ W	Villa Rosa earth barrier (5.5 km long) separates the El Guájaro reservoir from the Dique channel. Zone with high presence of macrophytes.

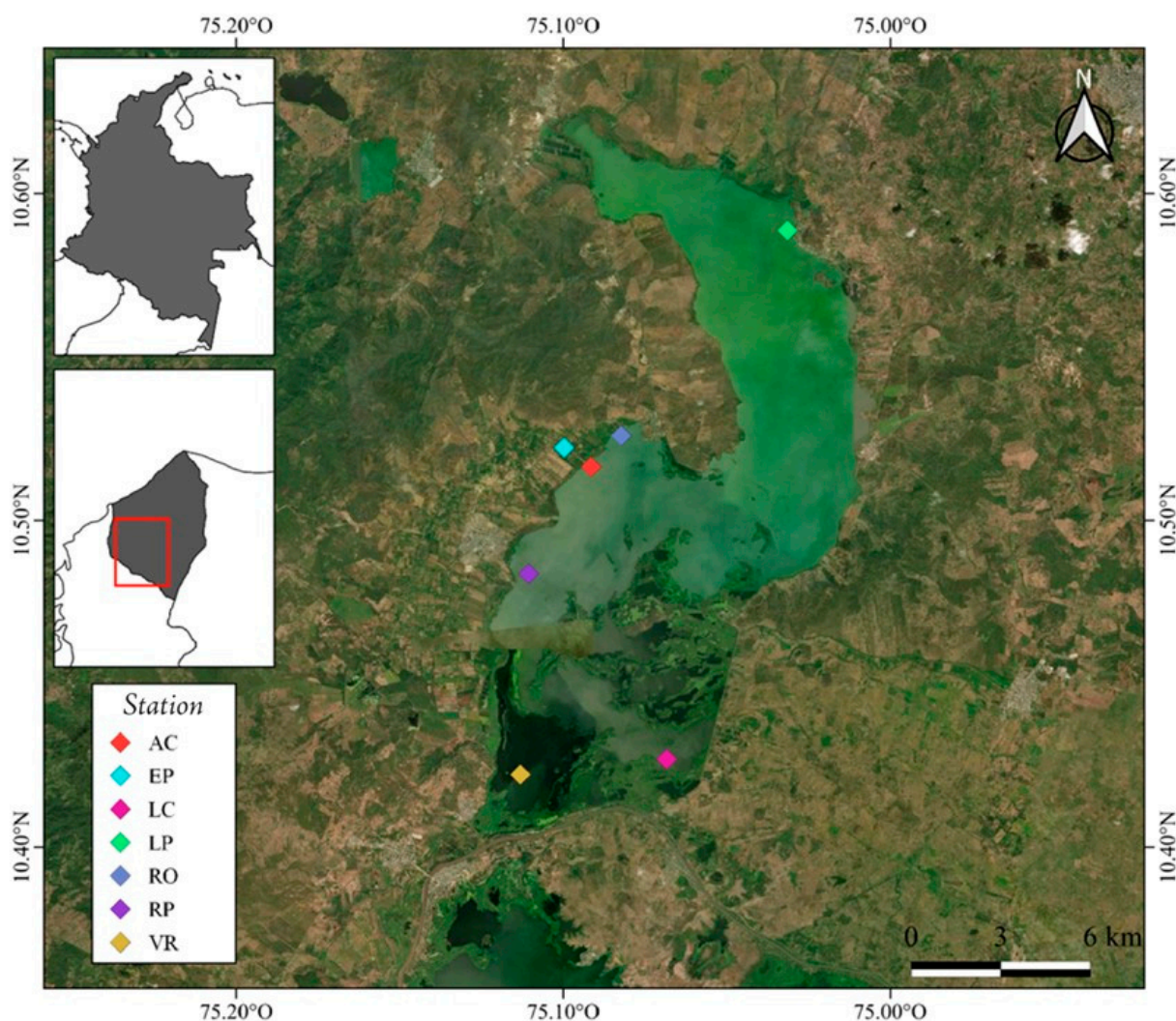


Figure 1. Distribution of monitoring stations in El Guájaro reservoir, northern Colombia (2015–2019).

2.3. Isolation and Species Identification

Water samples were collected for the identification and quantification of cyanobacteria using a Van Dorn bottle (4 L) at a depth of one meter. To preserve the samples during transport to the laboratory, they were stored in 0.25 L amber bottles, adding 1% of Lugol's solution as a preservative [30].

The taxonomic identification was based on a thorough examination of the morphological characters, considering the following factors: (i) size and length of vegetative cells and heterocysts; (ii) shape and size of colonies or filaments; (iii) presence or absence of constrictions in the wall structure; (iv) number of trichomes per filament; and (v) presence or absence of a sheath. For this purpose, recognized taxonomic keys were applied [30–34], as well as the use of the AlgaBase (www.algaebase.org (accessed on 25 June 2023)) and the NCBI taxonomy database (www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi (accessed on 25 June 2023)).

Each sample volume was gently homogenized by sedimenting a volume of 100 mL in Utermöhl chambers, within 48 h. Subsequently, the individuals were counted, and the entire surface of the chamber was observed at 400X under an inverted microscope (Motic AE2000). Abundance was determined in terms of density, expressed in cells per milliliter (cell/mL), following the specifications of the Utermöhl method for the quantitative analysis of phytoplankton [35].

2.4. Alpha and Beta Diversity Indexes

An analysis of alpha and beta diversity indexes was performed to estimate the biological diversity of the cyanobacteria. For alpha diversity, the effective number of species was calculated as a measure of richness. The standardized method of Hill numbers was employed, enabling the quantification and comparison of diversity through a rarefaction analysis (interpolation) and extrapolation (prediction). This method incorporates three diversity measures: (⁰D) species richness, (¹D) Shannon diversity or effective number of abundant species, and (²D) Simpson diversity or effective number of dominant species [36].

To estimate diversity, the iNEXT package [36] in R v. 4.3 (R core Teams 2023) software [37] was utilized. This package utilizes the approach developed by Chao and Josh [38], to generate extrapolation and rarefaction sampling curves for the three orders of diversity (⁰D, ¹D, and ²D). Confidence intervals at a level of 95% were calculated for each diversity order [39].

Additionally, a beta diversity (β) analysis was performed to assess the dissimilarity between cyanobacterial communities within the reservoir. This analysis consisted of decomposing beta diversity (β_{sor}) into two components [40]:

$$(\beta_{sor}) = \text{nesting } (\beta_{nes}) + \text{turnover } (\beta_{sim})$$

These components provide information about the dissimilarity of the samples in terms of species richness, composition, and abundance. Sørensen's coefficient was used to calculate the occurrence data (presence–absence) and their respective abundances [40]. The analysis was performed using the Betapart package [41] in R v. 4.3 (R core Teams 2023) software [37].

The spatiotemporal variation of the cyanobacterial community was visualized through a non-metric multidimensional scaling analysis (NMDS), based on the Bray–Curtis similarity index [42]. This analysis was performed using the MASS [43] and Vegan packages [44], enabling the examination of similarities or differences among localities at spatial scales. The vectors and environmental factors were fitted to the NMDS ordination matrix using the “envfit” function from the Vegan package, considering the sampling year as the block stratum and utilizing 999 permutations. These analyses were conducted in R version 4.3 (R Core Team 2023).

To identify the effects of the climatic season (dry and rainy), years (2015–2019), and physicochemical variables (pH, DO, BOD₅, T, conductivity, and TSS), a generalized linear model (GLM) was utilized. The objective of the GLM was to evaluate how these factors influenced the abundance (N) and diversity (⁰D, ¹D, ²D) of cyanobacteria.

To analyze the abundance and richness (⁰D), the glmr function of the lme4 package was utilized, assuming a Poisson distribution [45]. For diversity measurements related to common species (¹D) and dominant species (²D), a normal or Gaussian distribution was assumed. To address collinearity between explanatory variables, a Pearson correlation test was performed using the cor.test function of the R Stats package. Lastly, each response variable final model was compared to a null model, and the best model was selected using the Akaike information criterion (AIC) [46].

3. Results

3.1. Analysis of Physicochemical Parameters

To provide an overview, the mean of each physicochemical variable recorded throughout the study period was calculated (Table 2). The pH level of the reservoir varied across different climatic periods, ranging from 6.09 to 9.23. The overall average of this variable was 7.8 with a standard deviation of 0.95 during the rainy seasons, compared to 0.58 during the dry seasons. In terms of spatial distribution, the northern zone of the reservoir demonstrated elevated average pH values during the dry seasons (8.6), whereas the southern zone displayed slightly lower values compared to the rest of the system (Table S1).

Table 2. Variations in the parameters of pH, temperature, dissolved oxygen, conductivity, BOD5, and total suspended solids (TSS), at the surface water level of El Guájaro reservoir, during the period 2015–2019. For each variable, the mean, extreme values, and standard deviation were measured during both the dry and rainy seasons.

Year		pH		Temperature °C		Dissolved Oxygen (mg/L)		Conductivity (µS/cm)		BOD5 (mgO ₂ /L)		TSS (mg/L)	
		Dry	Rain	Dry	Rain	Dry	Rain	Dry	Rain	Dry	Rain	Dry	Rain
2015	Min	7.24	6.21	27.77	25.23	4.44	5.93	544.77	642.00	3.44	5.04	9.87	17.27
	Max	8.47	8.31	31.41	28.57	7.45	6.59	1184.67	877.33	5.93	6.04	33.04	36.38
	Mean	7.88	6.94	30.01	27.06	5.90	6.21	930.83	763.10	4.57	5.60	21.45	30.30
	St.des	0.39	0.76	1.10	1.36	0.97	0.26	217.89	91.84	0.93	0.41	8.64	6.23
2016	Min	7.49	6.09	29.76	25.45	3.63	5.21	736.33	345.72	4.15	3.50	28.08	9.20
	Max	8.73	8.31	31.14	27.95	6.07	7.91	1263.33	838.67	6.64	4.11	48.00	24.41
	Mean	8.22	7.03	30.55	26.20	5.17	6.25	940.10	609.69	5.17	3.86	37.17	15.36
	St.des	0.47	0.82	0.53	0.83	1.27	0.88	184.34	193.69	0.86	0.26	7.04	5.09
2017	Min	7.06	7.81	27.98	29.87	3.56	4.72	172.21	727.33	3.86	3.01	8.53	27.38
	Max	8.39	9.23	31.35	31.13	6.56	6.92	1089.00	918.00	5.68	5.87	34.13	35.45
	Mean	7.47	8.77	28.78	30.36	4.72	6.21	430.38	802.10	4.29	4.57	16.01	29.26
	St.des	0.48	0.53	1.15	0.42	1.26	0.77	306.34	88.89	0.63	1.09	9.56	2.77
2018	Min	6.90	7.52	29.56	30.13	3.52	3.50	181.44	324.67	3.64	2.41	8.49	16.02
	Max	8.79	8.88	32.10	31.15	6.62	5.59	1080.33	1147.33	5.56	2.80	32.70	28.37
	Mean	7.62	8.31	30.58	30.46	4.74	5.11	547.89	723.29	4.22	2.65	16.66	24.44
	St.des	0.90	0.43	0.90	0.37	1.17	0.73	374.56	265.60	0.63	0.19	9.13	4.23
2019	Min	7.62	7.86	29.42	30.13	4.21	4.08	499.11	292.67	4.99	2.34	28.01	18.67
	Max	8.53	8.93	31.28	33.80	5.36	5.65	1034.66	1138.33	7.26	2.90	43.10	28.00
	Mean	7.97	8.38	30.40	32.80	4.70	4.82	730.15	720.24	5.92	2.61	34.40	22.81
	St.des	0.34	0.34	0.65	1.32	0.45	0.91	259.18	272.53	0.73	0.22	7.55	4.34

The average water surface temperature was 30 °C, with the lowest recorded temperature occurring in November 2015 (25.2 °C), coinciding with the onset of rainfall in the region. The highest temperature, 33.8 °C, was recorded in the northern area of the reservoir in 2019, marking the beginning of the rainy season.

In relation to dissolved oxygen, the highest values were observed during the rainy season, mainly within the central zone of the reservoir. This pattern was notably pronounced at the RE station, which also recorded the highest population abundances during both dry and rainy periods. However, measurements at the Las Compuertas station (LC), located in the southern part of the reservoir, consistently showed low values during the rainy periods of 2018 and 2019 (Table S1).

This parameter presents a correlation with BOD5, whose highest records were during the dry season in 2019 towards the southern zone (7.26 mgO₂/L), and greatly changing in the rainy season.

The data obtained reveal an average concentration of total suspended solids above 22 mg/L, with fluctuations spanning from 8.45 to 48.0 mg/L. In particular, the northern zone consistently presented high levels of suspended solids during the dry seasons. Considering the entire study period, the mean conductivity values approached 660 µS/cm. However, a comparison among the different sectors revealed that the northern zone steadily exhibited the highest conductivity levels, while the central zone showed relatively stable values, and the southern zone had the lowest values. The maximum recorded conductivity was 1263.33 µS/cm during the dry season of 2016, while the minimum was 172.2 µS/cm in the southern part of the gates in 2017.

3.2. Analysis of Cyanobacterial Abundance

The results of this study present an analysis of the composition, distribution, and abundance of the cyanobacterial communities of the El Guájaro reservoir. The results reveal significant spatiotemporal variations and cyclical patterns that coincide with climatic seasons. A total of 86 taxa were identified, belonging to 12 orders and 42 genera. Among

the species found, several are recognized as forming blooms and potentially produce toxins. These include *Microcystis aeruginosa*, *Planktothrix agardhii*, *Limnithrix redekei*, *Dolichospermum circinale*, *Aphanizomenon flos-aquae*, *Pseudanabaena catenata*, *Raphidiopsis raciborskii*, and *Raphidiopsis curvata* (Figure S1). Additionally, the genera *Pormidium*, *Nostoc*, and *Leptolyngbya*, which are abundant in the system, have many species reported as toxin producers (Table 3).

Table 3. Percent abundance and relative frequency of cyanobacteria found in El Guájaro reservoir (2015–2019), and a compendium of toxin types associated with the identified genera.

Order	Specie	Relative Abundance (%)	Relative Frequency (%)	Toxin Type *	Ref.
Chroococcales	<i>Aphanocapsa delicatissima</i>	2.72	0.66	microcystin	[47]
	<i>Aphanocapsa grevillei</i>	2.22	0.93		
	<i>Aphanocapsa</i> sp.	3.23	1.72	microcystin	[48]
	<i>Merismopedia</i> sp.	1.23	2.12		
	<i>Snowella lacustris</i>	0.51	0.66		
	<i>Synechocystis</i> sp.	2.08	0.93		
	<i>Aphanothece</i> sp.	2.11	1.32	microcystin	[49]
	<i>Aphanothece stagnina</i>	0.65	0.26		
	<i>Chroococcus dispersus</i>	1.01	1.06		
	<i>Gloeocapsa</i> sp.	0.74	1.59		
	<i>Microcystis aeruginosa</i>	3.78	2.25	microcystin	[4]
	<i>Microcystis flos-aquae</i>	0.08	0.13	microcystin	[48]
	<i>Microcystis</i> sp.	0.46	0.40	microcystin	[48]
	<i>Radiocystis fernandoi</i>	0.55	0.66	microcystin	[50]
	<i>Chroococcus dispersus</i>	1.01	1.06		
Synechococcales	<i>Synechococcus rubescens</i>	0.95	0.66		
	<i>Synechococcus</i> sp.	2.26	1.72	microcystin	[48]
	<i>Jaaginema</i> sp.	0.13	0.53		
Nostocales	<i>Anabaena</i> sp.	0.06	0.66	anatoxin-a (S)	[51]
	<i>Anabaenopsis</i> sp.	0.17	0.40	microcystin	[48]
	<i>Aphanizomenon flos-aquae</i>	0.41	0.53	saxitoxin	[52]
	<i>Aphanizomenon gracile</i>	0.02	0.13	microcystin	[53]
	<i>Aphanizomenon</i> sp.	0.19	0.40	microcystin saxitoxins	[52,54]
	<i>Calothrix</i> sp.	0.46	0.79	microcystin	[49]
	<i>Cylindrospermopsis</i> sp.	2.00	2.12	cylindrospermopsin	[52]
	<i>Raphidiopsis raciborskii</i>	3.29	2.51	saxitoxins	[48,55]
				cylindrospermopsin	
	<i>Raphidiopsis curvata</i>	3.37	2.51	cylindrospermopsin	[48]
	<i>Raphidiopsis</i> sp.	0.40	0.53	microcystin	[48]
				cylindrospermopsin	
	<i>Dolichospermum circinale</i>	0.34	1.06	microcystin saxitoxin	[56]
				anatoxin-a (S)	
	<i>Dolichospermum crassum</i>	0.99	0.53	microcystin	[48,56]
				anatoxin-a (S)	
	<i>Dolichospermum flos-aquae</i>	0.55	0.26	anatoxin-a (S)	[48,57]
	<i>Dolichospermum sigmoides</i>	0.55	0.53	microcystin anatoxin	[58]
	<i>Dolichospermum affinis</i>	0.62	0.40	microcystin anatoxin	[48]
	<i>Dolichospermum</i> sp.	0.91	1.19	microcystin	[48]
	<i>Dolichospermum spiroides</i>	0.20	0.26	anatoxin-a (S)	[58]
	<i>Cylindrospermum</i> sp.	0.07	0.26		
	<i>Nodularia</i> sp.	0.02	0.13	microcystin nodularin	[48]
	<i>Nostoc commune</i>	3.90	3.97		
	<i>Nostoc muscorum</i>	2.00	1.59	microcystin	[49]
	<i>Nostoc</i> sp.	1.29	1.72	microcystin anatoxin-a	[4]
	<i>Scytonema</i> sp.	0.53	1.32	BMAA saxitoxin	[4,49]
	<i>Tolypothrix</i> sp.	0.44	0.66	microcystin	[51]
	<i>Stigonema</i> sp.	0.46	1.19		

Table 3. Cont.

Order	Specie	Relative Abundance (%)	Relative Frequency (%)	Toxin Type *	Ref.
Leptolyngbyales	<i>Leptolyngbya rivulariarum</i>	0.11	0.13	microcystin	[59]
	<i>Leptolyngbya</i> sp.	4.68	5.16		
	<i>Leptolyngbya subtilis</i>	1.69	0.93		
	<i>Leptolyngbya valderiana</i>	1.12	1.32		
	<i>Pseudophormidium tenue</i>	1.04	0.79		
	<i>Pseudophormidium viride</i>	0.54	0.79		
	<i>Pseudophormidium</i> sp.	0.86	1.46		
	<i>Pseudophormidium purpureum</i>	0.12	0.13		
Pseudanabaenales	<i>Limnothrix planktonica</i>	1.40	2.12	microcystin	[48]
	<i>Limnothrix redekei</i>	0.75	1.32		
	<i>Limnothrix</i> sp.	0.07	0.66		
	<i>Pseudanabaena catenata</i>	8.85	6.22	microcystin	[60]
	<i>Pseudanabaena galeata</i>	0.54	0.13	microcystin	[60]
	<i>Pseudanabaena limnetica</i>	0.33	0.40		
	<i>Pseudanabaena mucicola</i>	0.70	0.66		
Oscillatoriales	<i>Arthrospira jenneri</i>	0.20	0.93	microcystin anatoxin-a microcystin	[4,49] [49]
	<i>Arthrospira platensis</i>	0.11	0.66		
	<i>Arthrospira skujae</i>	0.02	0.26		
	<i>Arthrospira</i> sp.	0.04	0.40		
	<i>Cyanotheca</i> sp.	1.26	1.19		
	<i>Oscillatoria limosa</i>	0.27	0.93		
	<i>Oscillatoria</i> sp.	0.99	3.70		
	<i>Phormidium articulatum</i>	1.86	2.25		
	<i>Phormidium breve</i>	0.06	0.13		
	<i>Phormidium arthrospiroides</i>	1.11	1.06		
	<i>Phormidium formosum</i>	0.18	0.13	anatoxin-a homoanatoxin	[4]
	<i>Phormidium papyraceum</i>	4.26	3.57		
	<i>Phormidium</i> sp.	4.91	4.10		
	<i>Phormidium granulatum</i>	0.06	0.13	microcystin microcystin anatoxin-a	[61] [54]
	<i>Planktothrix agardhii</i>	4.32	0.13		
	<i>Planktothrix</i> sp.	0.79	3.70		
Coleofasciculales	<i>Symploca dubia</i>	0.04	0.13		
	<i>Symploca</i> sp.	0.22	0.53		
Spirulinales	<i>Spirulina</i> sp.	0.02	0.13		
	<i>Spirulina subsalsa</i>	0.08	0.40		
Gomontiellales	<i>Komvophoron</i> sp.	0.31	0.66		
	<i>Komvophoron crassum</i>	0.13	0.13		
Nodosilineales	<i>Romeria leopoliensis</i>	2.58	1.46		
	<i>Romeria</i> sp.	2.73	2.12		
Geitlerinematales	<i>Geitlerinema</i> sp.	0.24	0.40		
	<i>Geitlerinema unigranulatum</i>	0.04	0.13		
Pleurocapsales	<i>Pleurocapsa</i> sp.	1.30	1.85		
	<i>Hyella</i> sp.	0.16	0.40		

Note: * Most important toxin type reported.

The species with the highest frequency at the sampling sites and the most abundant individuals were *Pseudanabaena catenata* and *Phormidium papyraceum*. Filamentous genera exhibited greater abundance and prevalence. Nevertheless, coccoid species of the genera *Microcystis*, *Aphanocapsa*, and *Synechocystis* were frequently observed in codominance with filamentous species. Importantly, this codominance was not constant throughout the year, as it varied in response to changes in climatic seasons.

During the 2015 dry season, the study recorded the highest number of individuals, with a count of 4946 cells/mL, and a mean abundance of 540 cells/mL (Table S2). The dominant and abundant species during this period included *Pseudanabaena catenata*, *Phormidium* sp., *Aphanocapsa* sp., *Limnothrix planktonica*, and *Synechocystis* sp. However, a significant reduction in populations was observed during the subsequent rainy season of this year, with an average count of 166.4 cells/mL (Table S2). In this period, dominance shifted to *Cylindrospermopsis* sp., *Pseudanabaena catenata*, and *Planktothrix agardhii*.

In 2017, the study recorded the lowest cell density, with an average of 99.4 cells/mL, and a dominance of *Phormidium articulatum*, *Nostoc commune*, *Merismopedia* sp. and *P. catenate* was observed. Except for what occurred in 2015, the cyanobacterial community in the reservoir showed a trend of higher cell numbers during wet seasons (Figure 2). Beyond the analysis of temporal distribution, this study examined the spatial characterization of the reservoir, revealing that the stations located in the central zone generally exhibited a higher abundance of cyanobacteria.

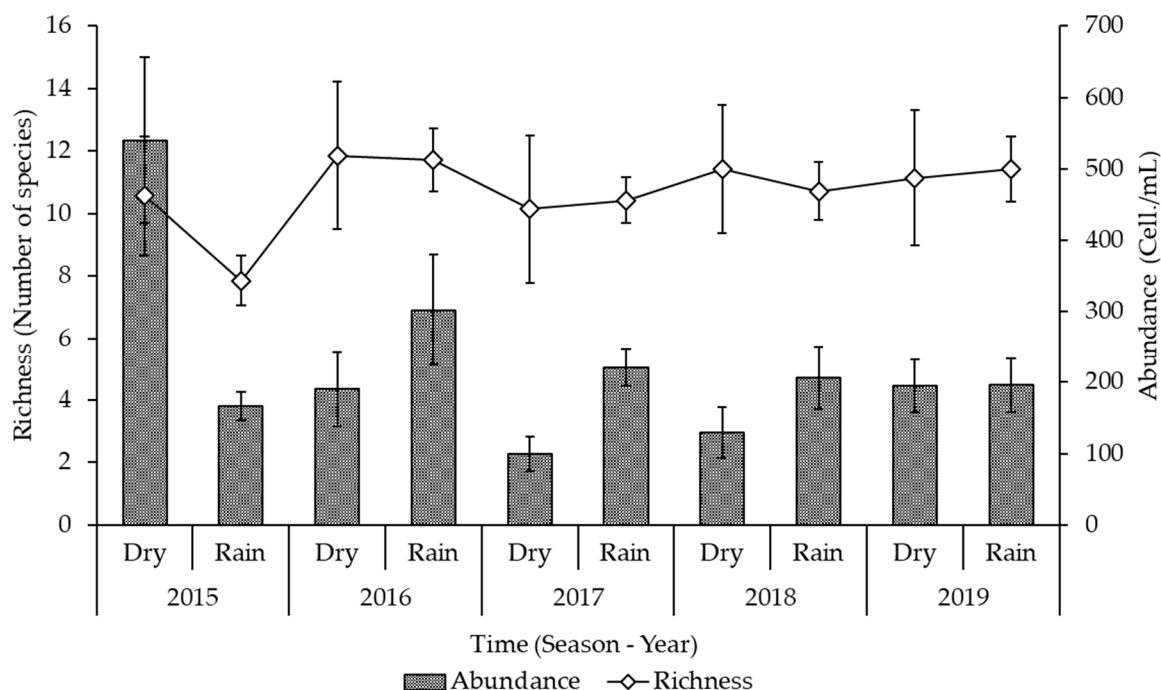


Figure 2. Abundance and richness of planktonic cyanobacteria species in the El Guájaro reservoir (Colombia) during the dry and rainy seasons from 2015 to 2019.

3.3. Cyanobacteria Diversity Analysis

The system exhibited relatively homogeneous species richness (Figure 2). Spatial variations were observed, indicating a preference of certain species for specific areas within the system, resulting in patterns of dominance in particular sites of the reservoir. This consistent pattern was also observed during seasonal changes when certain species disappeared, suggesting that cyclical behavior was associated with seasonal variation.

Higher species richness (0D) was observed in 2016 and 2019, mainly associated with the middle zone of the reservoir (Figure 3; Table S2). The pulses of higher abundance were associated with the presence of species that, in addition to being numerous, were dominant. The central zone of the reservoir had a higher species diversity than the northern and southern zones, which presented lower abundance indices associated with representative numbers of common species.

The genus *Phormidium* presented the highest species richness, while the most abundant and frequent species in both the dry and rainy seasons was *Pseudanabaena catenata*. It should be noted that species such as *Phormidium papyraceum*, *Planktothrix agardhii*, *Aphanocapsa delicatissima*, *Nostoc commune*, *Leptolyngbya* sp. and several species of *Dolichospermum*, were abundant in the northern and southern zones. However, the occurrence of *Aphanocapsa* and *Dolichospermum* was mainly associated with dry periods, while *Nostoc* species and *Planktothrix agardhii* showed dominance during the rainy season. The remaining species were frequent in both seasons.

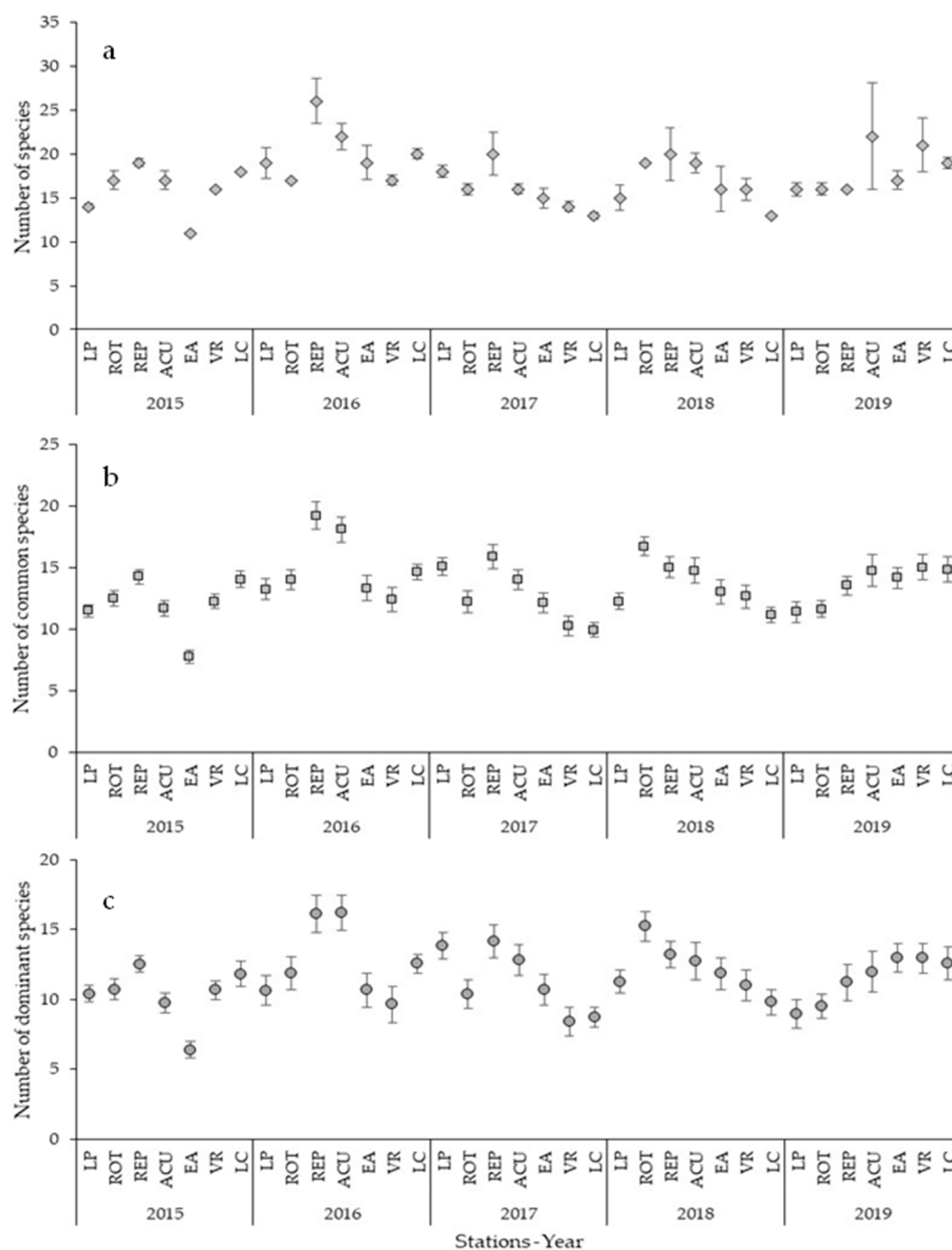


Figure 3. Alpha diversity analysis: (a) species richness (0D); (b) species in common (1D); and (c) dominant species (2D) of cyanobacteria found in different sampling sites of El Guájar reservoir during the years 2015 to 2019.

The results from the generalized linear model, as presented in Table 4, provide insights into the relationships among the variables and their effects on the abundance and diversity of cyanobacterial communities. The results show that the abundance is influenced by multiple factors. The interaction of these parameters in the aquatic environment is complex, and its impact can vary according to the specific conditions of each body of water. This is related to the environmental and anthropogenic alterations that exert pressure on the system.

Table 4. Generalized linear model (GLM) of the attributes of cyanobacterial communities found in El Guájaro reservoir (Colombia) during the years 2015 to 2019. Abundance and species diversity indices are related to physicochemical parameters and climatic seasons during the study time.

Response Variable	Factor/Explanatory Variable	lr × 2	Df	Pr(>Chisq)
N (Abundance)	Season	248.020	1	$2.20 \times 10^{-16} *$
	Site	380.940	6	$2.20 \times 10^{-16} *$
	Year	32.610	1	$1.13 \times 10^{-8} *$
	Oxygen	16.560	1	$4.71 \times 10^{-5} *$
	Temperature	135.950	1	$2.20 \times 10^{-16} *$
	BOD5	49.560	1	$1.93 \times 10^{-12} *$
	Season * Year	82.050	1	$2.20 \times 10^{-16} *$
	Season * Oxygen	2.890	1	0.089
	Season * Temperature	141.260	1	$2.20 \times 10^{-16} *$
	Site * BOD5	205.030	6	$2.20 \times 10^{-16} *$
	Site * Temperature	157.210	6	$2.20 \times 10^{-16} *$
⁰ D (Richness)	Season	4.045	1	0.044 *
	Year	1.051	1	0.305
	Site	4.901	6	0.556
	Conductivity	0.221	1	0.637
	BOD5	0.021	1	0.883
	pH	0.007	1	0.931
	Temperature	0.042	1	0.836
	Season * Year	0.855	1	0.355
	Year * Site	4.029	6	0.672
	Season * Conductivity	1.106	1	0.292
	Season * BOD5	0.288	1	0.591
	Site * Conductivity	2.929	6	0.817
	Season * pH	1.390	1	0.238
	Season * Temperature	2.285	1	0.130
¹ D (Common species)	Year	1.140	1	0.285
	Season	0.150	1	0.698
	Conductivity	2.991	1	0.084
	pH	0.818	1	0.365
	Temperature	1.244	1	0.264
	Year * Season	12.974	1	0.003 *
	Season * Conductivity	2.353	1	0.125
	Season * pH	8.329	1	0.004 *
	Season * Temperature	4.280	1	0.039 *
	Year * Conductivity	2.603	1	0.106
² D (Dominant species)	Season	5.910	1	0.015 *
	pH	1.619	1	0.203
	Temperature	1.544	1	0.214
	Conductivity	2.277	1	0.131
	Year	2.741	1	0.097
	Conductivity * Year	4.405	1	0.035 *
	Season * Year	17.345	1	0.031 *
	Temperature * Year	3.537	1	0.059
	Season * pH	4.203	1	0.040 *
	Season * Temperature	3.416	1	0.064

Note: *. Right column, significant values: p -value < 0.05.

In the reservoir, species richness (⁰D) demonstrated a correlation with climatic seasons, indicating a dependence on seasonal changes. In contrast, the distribution of common species (¹D) and taxa dominance (²D) appeared to be influenced by variations in temperature, conductivity, and pH level during the transition from drought to precipitation.

The observation of succession processes between potentially toxic species, including *Microcystis aeruginosa* and *Dolichospermum circinale*, was notable. These species primarily emerged within the northern and central zones of the reservoir, where elevated pH and conductivity levels were observed during the dry season. In particular, the northern part of the reservoir showed greater dominance of the genus *Microcystis*, which prevailed even until the beginning of the rainy season.

Beta Diversity: Cyanobacterial Turnover and Nestedness

The analysis of nesting and turnover has been employed as a tool to understand the factors that influence the presence of a species within a particular spatial and temporal context. The dynamics of cyanobacterial turnover and nestedness are illustrated in Figure 4. The beta diversity analysis has revealed that species turnover significantly contributes to dissimilarities observed among cyanobacterial communities in the El Guájaro reservoir.

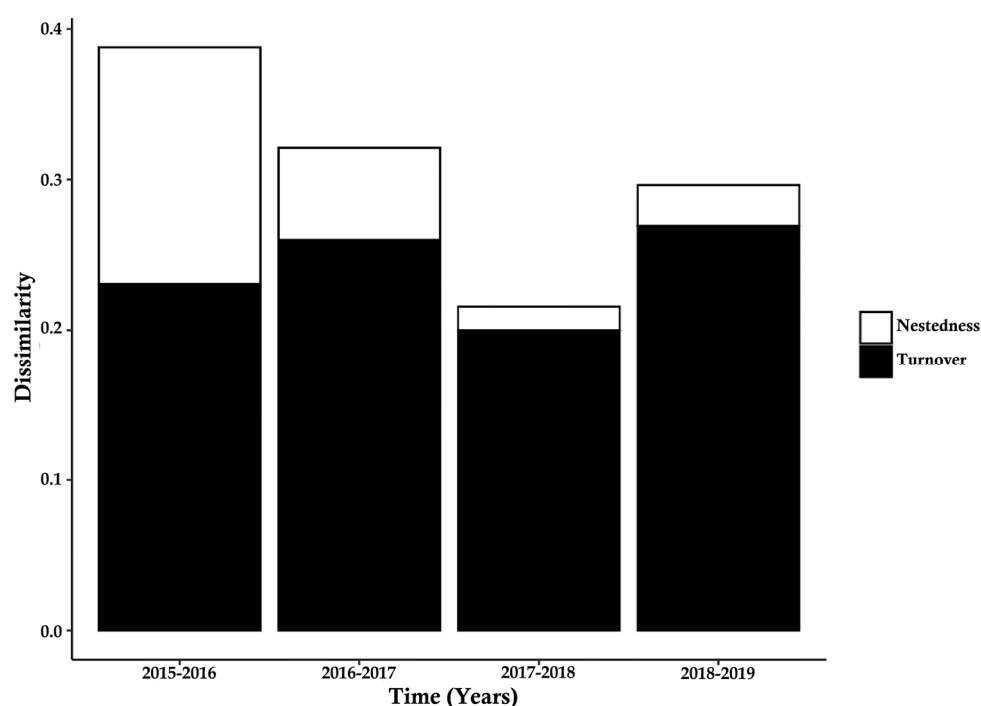


Figure 4. Estimation of beta diversity by turnover and nestedness in the species composition of cyanobacterial communities in El Guájaro reservoir during the 2015–2019 period.

Notably, the most significant dissimilarity was observed between the 2015 and 2016 populations, presenting a β_{sor} value of 0.38. This value indicates a nesting index of $\beta_{nes} = 0.36$, alongside a turnover index of $\beta_{sim} = 0.23$. This divergence could be attributed to a tendency among the highly abundant or common species to reside in areas characterized by a certain degree of isolation, driven by either physical factors or specific environmental conditions. Another possible explanation could be that the predominant species are capable of enduring adverse and highly fluctuating conditions.

Conversely, the lowest dissimilarity, indicated by an index of 0.21, was observed between 2017 and 2018. It should be noted that the precipitation and drought regimes in 2017–2018 remained within the typical range for the region, which could explain the maintenance of species richness.

The turnover pattern observed in the populations during 2018 and 2019 allowed us to identify shifts in community composition and structure. The results demonstrate that, despite population variations, the system does not reach a state of disequilibrium due to species exchanges that may be fulfilling similar functions within the community.

3.4. Non-Parametric Multidimensional Scaling Analysis

A marked distinction was observed between the cyanobacterial communities in the El Guájaro reservoir, directed by dry and rainy seasons (Figure 5a). The taxa evaluated during the study showed distinct patterns in terms of abundance and richness. Although, despite fluctuations in populations, a significant number of shared species were identified in 2015, 2016, and 2019, particularly during dry seasons. Species that were present during the rainy periods of 2017 and 2018 appeared to have their own characteristics and were isolated in a separate component (Figure 5b).

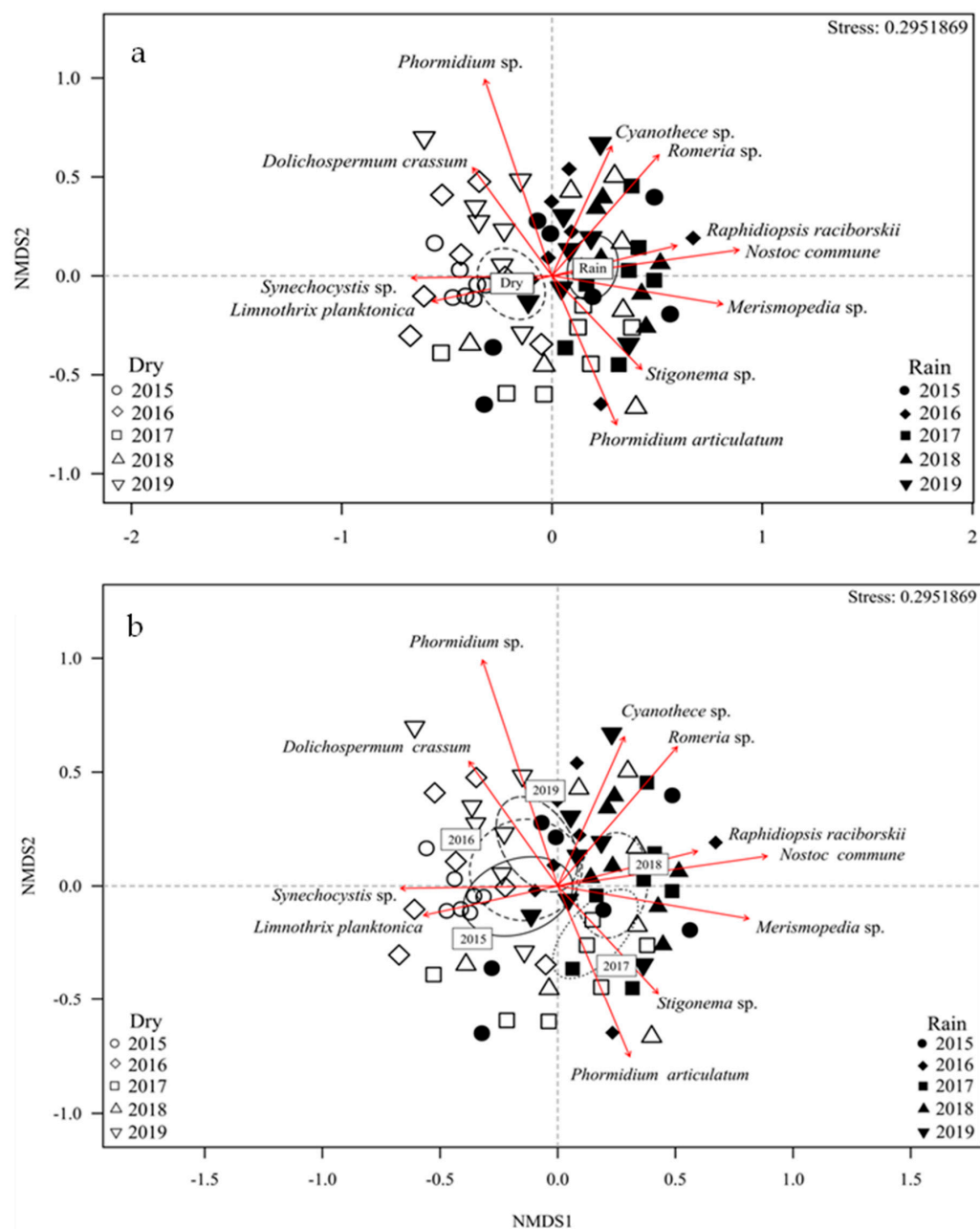


Figure 5. Non-parametric multidimensional scaling analysis of the cyanobacterial community in El Guájaro reservoir. (a) NMDS based on the effect of climatic epochs (rainfall and drought) and (b) NMDS based on the differences of the communities present in the years of the study (2015–2019).

Not all cyanobacteria maintained the same response to seasonal change. Genera such as *Merismopedia*, *Cyanothece*, and *Stygonema* showed sporadic appearances in the reservoir without significant abundance. However, their presence or absence could have influenced the measurement of species diversity, leading to the marked divisions that were evident during the rainy periods of 2017 and 2018 (Figure 5b). Similarly, *Limnothrix planktonica* and *Synechocystis* sp. are species with distinctive abundances, but they did not remain frequent either spatially or temporally.

The study centered on genera that were widely distributed in the reservoir with high relative abundances, and which are recognized in the literature as potential toxin producers and frequent bloom formers. The genera that met these criteria were *Dolichospermum*, *Leptolyngbya*, *Microcystis*, *Nostoc*, and *Phormidium*.

Our findings indicated that approximately 31% of *Dolichospermum* species were identified in the northern sector of the reservoir, whereas 33% were linked to stations in the central zone. In the northern sector of the reservoir, *Microcystis* constituted 45% of the population, whereas at stations in the central zone, it accounted for 22% of the total abundances. *Leptolyngbya* species exhibited the highest prevalence at stations located in the south of the reservoir, comprising 41%, followed by *Nostoc* species at 24%. *Phormidium* maintained a distribution mainly associated with the central and southern parts of the reservoir.

The environmental variables that have a significant influence on species distribution, depending on the climatic season, are presented in Figure 6. Among these variables, the most influential are DO, conductivity, BOD5, and TSS, which tend to exert a greater influence during the dry season.

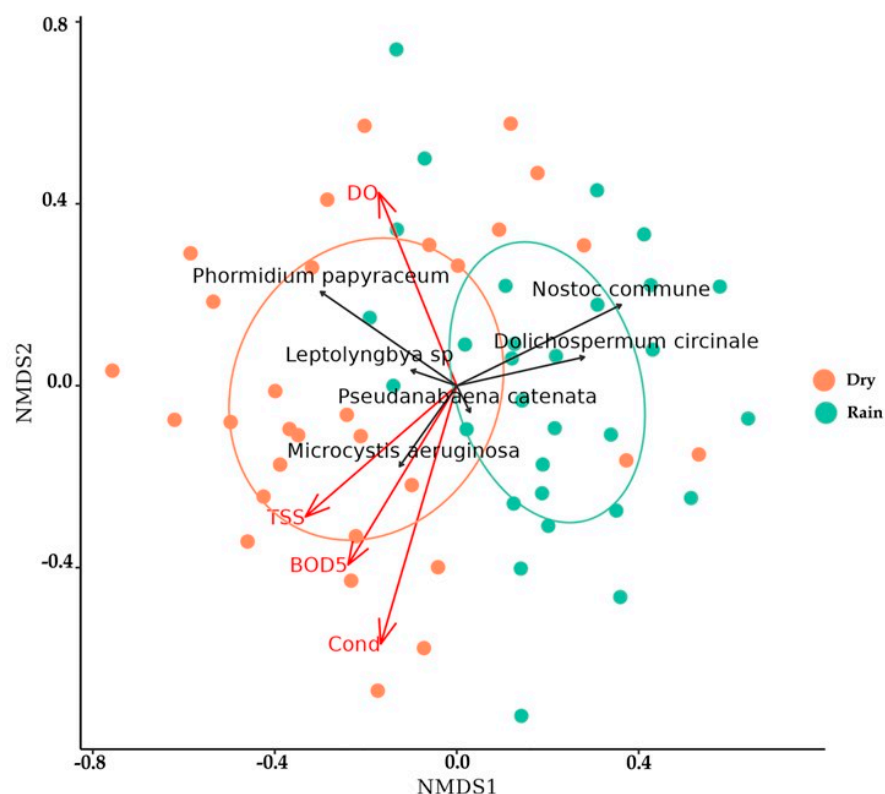


Figure 6. NMDS non-metric multidimensional scaling analysis of the species of cyanobacteria of interest, considering the interaction with relevant environmental variables and confidence ellipses for climatic periods.

Similar to other cyanobacteria, *Microcystis aeruginosa* is susceptible to fluctuations in water conductivity, TSS, and BOD5. Elevated levels of these parameters often indicate a higher presence of ions, nutrients, salts, minerals, and decomposing organic matter in the water. This pattern is consistently observed in the El Guájaró reservoir, especially during dry seasons, establishing an ideal environment for the growth and proliferation of *Microcystis aeruginosa* and other toxic cyanobacteria.

4. Discussion

Climatic seasons have an influence on the physicochemical parameters and the dynamics of cyanobacterial populations in the reservoir.

The abundance of cyanobacteria in the El Guájaró reservoir does not appear to be the result of a specific environmental factor but rather the result of a complex interaction between temperature, conductivity, pH, and precipitation patterns, which in turn are related to the trophic state of the reservoir. The diverse nature of cyanobacteria, including their functions and characteristics, contributes to the dynamics of reservoir communities. Furthermore, this contribution depends on their ability to respond rapidly to environmental changes and fluctuating conditions in the system.

In general, the El Guájaró reservoir presented high temperatures that, at surface level, are subject to the retention of more heat units by contact with the atmosphere [62]. The northern and central zones showed higher average values for this parameter, both in dry and rainy periods. This factor may be directly related to the hydrodynamics of the reservoir, which is influenced by the direction and speed of the winds, depending on the season, the high radiation in the area, the bathymetry of the system, and factors such as the opening and closing times of the floodgates.

According to the reports from the regional environmental authority (CRA), which is responsible for monitoring the reservoir, the water column is marked by thermal stratification conditions, characterized by a high degree of eutrophication [18]. The importance of the temperature in the reservoirs is that it directly influences the concentration of nutrients and dissolved oxygen, as well as the release of metals from sediments, affecting primary production [63].

In relation to the above, local meteorological conditions are highly influenced by the El Niño and La Niña phenomena in the region. Factors that vary with seasonality regulate the selection of species that adapt to the changes by their influence on growth [64,65].

It is possible that the physicochemical conditions that prevailed in the reservoir during the 2015 dry season, along with other factors not considered in this study, were responsible for the higher abundance of cyanobacteria found compared to the other years studied. However, when the conditions of the long dry season changed and low rainfall began, there may have been a washout effect on the populations, which could explain the decline in abundance and species richness.

The physicochemical and biological factors analyzed show a differentiated spatial gradient between the areas studied. The values of the parameters tend to increase as the points approach the northern zone, in contrast to the abundance and diversity of cyanobacteria. During the study period, conditions in the northern zone favored the dominance of several species.

According to historical reports, fluctuations in total suspended solids in the reservoir averaged 22.7 mg/L [24,25]; however, in the northern zone of the reservoir, we found average values above 30 mg/L during the summer. The same trend was observed for BOD5 in both the northern and southern zones during the dry season, indicating a higher accumulated organic matter content [66].

In general, it was observed that BOD5 presents fluctuating gradients along the system, possibly caused by anthropogenic and natural disturbances that exceed the regulatory capacity of the system. Therefore, organisms with high adaptive flexibility, such as cyanobacteria, have the capacity to overcome these agents and present considerable abundances.

Turbidity in the El Guájaro reservoir is a factor that favors populations of filamentous cyanobacteria, which predominate in this system, mainly due to their maximum linear dimension and surface/volume ratio, which make them good light receptors [67]. Studies in different tropical areas have shown that the dominance of cyanobacteria can be maintained throughout the year with little change; however, water quality and reservoir ecology in arid tropical areas are determined by dry periods that lead to eutrophication and cyanobacterial dominance [67,68].

Monitoring and reports of toxic cyanobacteria in Latin America are scarce, providing only a superficial view of the subject. The countries with the most official reports and scientific publications are Brazil, Argentina, Chile, and Uruguay [67]. In Colombia there are few records of cyanobacterial blooms, and the available reports are mainly associated with aquaculture activities, estuarine zones, and mountain reservoirs.

Despite the importance of this reservoir on the Colombian Atlantic region, there is a gap in the research on the dynamics of cyanobacteria populations, their toxin production, and the potential risks they pose to the health of the communities. These communities depend on the reservoir for various purposes, including water consumption, fishing, and agricultural practices.

It is important to note that the El Guájaro reservoir is included in local policies aimed at promoting fish farming as a part of the food security for the region. Therefore, it is essential to understand the behavior of cyanobacteria in this system, closely monitor the occurrence of blooms, and implement management plans that include bloom control.

In Colombia there is no official registry of harmful algal blooms and there is a lack of government regulations for their monitoring and control [68]. Existing studies in the country have provided limited information, identifying potentially toxic species within genera such as *Microcystis*, *Oscillatoria*, *Cylindrospermopsis*, and *Radiocystis* as potentially toxic [67,69].

4.1. Toxic Blooms in El Guájaro Reservoir

Nitrogen-fixing cyanobacteria such as *Dolichospermum* and *Cylindrospermopsis* bloom in the dry season, favored by thermal stratification and stability in the water column [70]. *Cylindrospermopsis*, on the other hand, has advantages that allow it to dominate in turbid systems. However, species of these genera can compete under nitrogen-depleted conditions after a long period of stratification. Although the genus *Microcystis* is more associated with the dry season, it can also proliferate in rainy periods due to the high availability of nutrients that become available after rainfall [71].

In 2019, the predominant species were *Microcystis aeruginosa*, *Dolichospermum crassum*, *Dolichospermum circinale*, and *Phormidium* sp. The existence of seasonal succession processes among the species found has been demonstrated [70,72,73]. It was possible to identify codominance in two pulses of toxic blooms recorded on 20 March and 16 April 2019 (dry season), dominated by *Dolichospermum circinale* (1.4×10^{-5} cells/mL) and *Microcystis aeruginosa* (2.1×10^{-5} cells/mL); these caused the death of more than 40 cattle and other animals on the northeast bank of the reservoir, near the village of Aguada de Pablo, in the vicinity of La Peña [74–76].

These taxa can simultaneously produce a variety of microcystins, anatoxins, and saxitoxins [77,78]. The causes that generated this event were not clearly identified by local authorities, suggesting a possible illegal discharge of wastewater. However, no analysis was performed to identify cyanotoxins. The detection and quantification of cyanotoxins require the use of specialized laboratories with expertise, as the techniques vary depending on the type of cyanotoxin and the sample matrix. This necessity entails a significant investment that, unfortunately, is not always accessible to all regions of the world.

Currently, the environmental authorities are conducting phytoplankton sampling and physicochemical parameter measurements, without clearly determining the relationship between these factors and the risks of the prevalence of toxic cyanobacteria in the area [27].

The complex situations that may influence the incidence of cyanobacteria in the El Guájaro reservoir will depend not only on reservoir management, but also on the different oscillations in extreme climatic events [79,80], which are increasingly irregular in this region of Colombia.

4.2. Reservoir Conditions That Favor the Presence of Potentially Toxic Species

The increase in water temperature and changes in precipitation cause dispersion patterns along the reservoir that favor the buoyancy of cyanobacteria, making them more efficient in their resistance and colonization processes [81], and enabling them to benefit from the thermal stratification generated in this system [18].

Quarries and agricultural activities are the main factors affecting the high pH level of the El Guájaro reservoir, especially in the central and southern areas, which may also affect the dynamics of heavy metals and pesticide residues. These pollutants enter the reservoir through sediment entrainment from the Magdalena River and terrestrial runoff [17,20,23]. These conditions apparently favor populations of the genus *Phormidium*, which is very abundant at almost all times of the year and whose masses are formed in areas with high agricultural activity and sediment input, leading to their abundance and providing them with adaptive advantages that increase the risk of anatoxin production [53].

It is known that *Microcystis* species are favored by a positive correlation with temperature and light intensity; these conditions directly affect both their cell density and the production of toxin variants [73]. This genus is favored by its surface/volume ratio, which helps them in the uptake of phosphorus and the production of allelochemical compounds [82,83].

Several of the genera found can grow in the same type of niche and adapt to different conditions of turbidity, temperature, and pH, as is the case with *Planktothrix*, *Cylindrospermopsis*, *Pseudanabaena*, and *Microcystis* [83–85].

The increase in *Microcystis* abundance within the northern region likely resulted from increased nitrogen inputs, primarily stemming from anthropogenic sources and agricultural activities in the surrounding areas. It is established that current fertilizers primarily consist of ammonium and urea, serving as significant nitrogen sources. *Microcystis* demonstrates the ability to assimilate urea as a nitrogen and carbon source, providing it with metabolic advantages [85].

In our study, we refrained from estimating nutrient levels, since these assessments are routinely conducted and documented in various studies conducted by the competent environmental authority. Over the course of a decade, these studies have consistently classified the trophic status of this system as eutrophic, especially emphasizing its greater impact in the northern region.

Another factor supporting the association of *M. aeruginosa* with the elevated conductivity and TSS levels in the El Guájaro reservoir is its demonstrated adaptability to brackish conditions. This species exhibits a notable plasticity through the overexpression of compatible solutes. These solutes act as substitutes for inorganic ions, playing a crucial role in regulating osmotic potential, maintaining turgor pressure, and preserving macromolecules. These compounds include cyanopeptoline C, glycerolipids, trehalose, sucrose, and various others [86].

The proliferation of *Leptolyngbya* is influenced by various physicochemical factors. These cyanobacteria can thrive in higher temperatures as well as in alkaline pH environments. Moreover, they exhibit a broad tolerance to water conductivity, although this measure can affect their proliferation capacity [87].

Nostoc forms colonies through the production of exopolysaccharides (EPS), providing it with a competitive advantage in environments with high turbidity and decomposing organic matter. It possesses adaptations to survive and thrive in conditions with elevated levels of BOD5. In addition to the ability to fix atmospheric nitrogen, *Nostoc* can benefit from environments with a high concentration of organic matter, thus utilizing nitrogen sources in the decomposition process. Certain species regulate EPS production in response

to their growth rate, acting as reservoirs for excess carbon in situations of imbalanced C/N metabolism [88–90].

The presence of potentially toxic species in the reservoir represents a latent risk, since the environmental factors found are favorable both for the increase of biomass and for the development of their dominance over other phytoplanktonic groups.

5. Conclusions

This study helps to identify the conditions that favor the proliferation of cyanobacteria in the El Guájar reservoir. There are no studies aimed at assessing the risk posed by cyanobacteria in the El Guájar reservoir to human health. Given the importance of this reservoir for the local economy and for the water consumption of some surrounding communities, a basic knowledge of cyanobacteria populations is necessary, since understanding their response to environmental factors is fundamental for establishing water management objectives.

The results indicate that seasonal changes mark trends in the distribution patterns and abundance of cyanobacteria in the photic zone of the reservoir. Filamentous species are dominant in the system and are mainly associated with turbid conditions and high temperatures. Most of them exhibit heterocysts and a high surface-to-volume ratio. Several genera of the order Nostocales, including *Dolichospermum*, *Aphanizomenon*, and *Calothrix*, as well as species of *Phormidium* and *Pseudanabaena*, are potential geosmin producers. *Pseudanabaena catenata* and several *Phormidium* species were the most abundant during the study period.

Considering that *P. catenata* not only produces toxins and geosmin, but also produces significant amounts of 2-methylisoborneol, a risk of economic losses develops for the aquaculture and fisheries sector in this reservoir, due to the earthy flavor that can be generated in fish products.

In general, the reservoir presented an abundance of species classified as potentially toxic, both in dry and rainy seasons. It is necessary to carry out continuous monitoring studies aimed at identifying and quantifying cyanobacteria in the Guájar reservoir, considering seasonal patterns, and including the identification of cyanotoxins to prevent risk to the local population.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15203696/s1>, Figure S1: Microphotographs of natural samples collected in El Guájar reservoir during the period 2015–2019; Figure S2: NMDS non-metric multidimensional scaling analysis of the cyanobacterial community with interaction between significant environmental variables and confidence ellipses of climatic epochs; Table S1: Mean values for physicochemical parameters evaluated during the climatic epochs of the years 2015 to 2019 in El Guájar reservoir, Colombia; Table S2: Abundance and species richness of cyanobacteria present in El Guájar reservoir, found from 2015 to 2019.

Author Contributions: T.-L.C.: Conceptualization (support), data curation (lead), methodology (lead), formal analysis (support), investigation (lead), software (support), validation (support), visualization (support), writing—original draft preparation (lead), and writing—review and editing (lead). O.-V.J.: Conceptualization (support), methodology (support), software (support), validation (support), formal analysis (support), investigation (lead), resources (lead), data curation (support), writing—review and editing (lead), visualization (support), supervision (lead), and funding acquisition (lead). All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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