# The first floristic study of freshwater dinoflagellates (Dinophyceae) in Colombia

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#### ABSTRACT

The first comprehensive study of dinoflagellate flora and their related environmental variables in reservoirs, swamps, and an insular lake of Colombia is presented. Fourteen Colombian water bodies were assessed. In each, water temperature, electric conductivity, oxygen saturation, turbidity, and apparent color were the physical and chemical variables measured. Twelve dinoflagellate taxa were recorded, indicating a considerable richness compared to similar surveys. Ensembles recovered showed a spatial structuration mediated by the type of the water bodies (reservoirs and swamps); environmental variables and species richness explained equally the differences among the water bodies. The dinoflagellate flora showed altitudinal segregation, with intermediate altitude systems displaying the highest richness values. A brief discussion about the geographical distribution of the species collected is offered. The study contributes to the knowledge of the ecological aspects of dinoflagellate flora and outlines preliminary biodiversity tendencies of ensembles in tropical water systems.

## INTRODUCTION

Dinoflagellates (Dinophyceae) are microorganisms of worldwide distribution (Taylor *et al.*, 2008). They occur from the polar zones to the tropics, from lowlands to high montane lands (Rengefors and Kremp, 2018), inhabiting all aquatic ecosystems but found mainly in oceans, lakes, ponds, swamps, and reservoirs. It is common to consider them ubiquitous; however, most species seem to be subcosmopolitan (Padisák, 2003). In other words, the species wide distributed usually are restricted to highly

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Floristic and ecological studies on dinoflagellates focus on sea species; most freshwater species are still understudied. The limited number of studies conducted in freshwater ecosystems reflects the lack of knowledge about continental dinoflagellates' ecological requirements (Grigorszky et al., 2003a; Rengefors and Kremp, 2018). Thus, the most relevant studies have emphasized community composition, geographical distribution, and blooms (Boltovskoy, 1983; Ling et al., 1989; Cavalcante et al., 2013, 2017; Craveiro et al., 2015). Although the biogeographical pattern distributions have not been unveiled, relevant information about the species' biology and life histories has been discussed (Pollingher, 1987; Moestrup and Calado, 2018). For example, Ceratium F. Schrank, 1793 and Peridinium Ehrenberg, 1830 are common and are by far the most studied taxa. In recent years, temperate-climate Ceratium hirundinella (O.F.Müller) Dujardin 1841 (Reynolds, 2006) have been recorded together with Ceratium furcoides (Levander) Langhans 1925 in tropical systems (Cavalcante et al., 2013). Peridinium willei Huitfeldt-Kaas 1900 is common and widely distributed in continental freshwater (Boltovskoy, 2003), and Peridinium volzii Lemmermann 1906 and Peridinium gatunense Nygaard 1925 are also of broad presence in tropical and subtropical regions (Boltovskoy, 1999). Few species are considered endemic or of restricted occurrence; one of these, Apocalathium baicalense (Kisselev & V. Zvetkov) Craveiro, Daugbjerg, Moestrup & Calado 2016, has only been recorded in Lake Baikal in Russia (Annenkova et al., 2015). Dinoflagellates also had been reported of forensic importance in drowing cases (Díaz-Palma et al., 2009).

Dinoflagellates are highly affected by the



environmental variables: temperature, salinity, pH, nutrients, and water turbidity (organic matter content) influence the presence of the species (Rengefors and Kremp, 2018). European studies pointed out that temperature and organic matter content were the main factors in the appearance of dinoflagellates (Grigorszky et al., 2003b). However, in Oceania, some species seem to prefer dystrophic waters (Ling et al., 1989). Finally, in subtropical regions, higher richness and biomass are related mainly to low temperatures and high nutrient content (Cardoso et al., 2010). Dinoflagellates display high mobility and dispersal capacity in the water column. It is common for high demographic explosions to cause blooms, which are more frequently reported as harmful in the sea (Anderson, 2007). Although freshwater dinoflagellates are not considered toxic, some studies warn that species like Apocalathium aciculiferum (Lemmermann) Craveiro, Daugbjerg, Moestrup & Calado 2016, have allelopathic toxins (Rengefors and Legrand, 2001), though others such as Naiadinium polonicum (Woloszynska) Carty 2014, have been related to high fish mortality (Roset et al., 2002; Hu et al., 2008).

In South America, dinoflagellate flora are still little studied; some surveys have been performed in Brazil and Argentina (Boltovskoy, 1999; Borics et al., 2005; Cavalcante et al., 2017), but none in the northwest region. Indeed, most of the Colombian studies regarding dinoflagellates are embedded in ecological assessments of the plankton of reservoirs ( Donato-Rondon, 1991; López-Muñoz et al., 2016) or included in checklists of sporadic studies carried out at different altitudes with different trophic conditions or in different systems (Ramírez et al., 2005; Jaramillo-Londoño and Aguirre-Ramírez, 2012; León-López et al., 2012). A very few national studies treat the autecology and occurrence of C. furcoides (Bustamante-Gil et al., 2012; Jaramillo-Londoño, 2018). Thus, the ecology and spatiotemporal distribution of dinoflagellates remain unknown in a highly diverse water resources region.

We aim to assess the spatial distribution of dinoflagellates and relate them to the environmental variables in some typical swamps, reservoirs, and lakes in Colombia. We are specifically interested in the distribution of species along altitudinal gradient. Finally, detailed and updated ecological information for the species collected is offered.

# **METHODS**

Sampling was performed from October 2016 to March 2017, and fourteen water bodies were assessed (Tab. 1): four are swamps located in the Caribbean region (northern); nine are reservoirs located in the Andean region (central and western); and one is an insular lake in the Pacific Ocean (southern; Fig. 1).

Three sampling sites were stablished by water body; in each, a vertical drag was executed along the euphotic zone by using a 20- $\mu$ m mesh net. The phytoplankton collected were transferred to a plastic jar and fixed with formalin (4% final cc).

In each sampling site, environmental variables - water temperature (°C), pH (pH units), electric conductivity ( $\mu$ S/cm), oxygen saturation (%), Secchi disk extinction depth (m), turbidity (nephelometric turbidity units, NTU), and apparent color (platinum-cobalt units) - were measured *in situ* at three depths with a multiparameter (Hach Corp.) and an MD 600 photometer (Lovibond). The first measurement was at the water surface, the second at the Secchi disk extinction depth, and the last at the depth of twice the Secchi disk extinction depth. These latter three variables were considered together as an indirect measure of organic matter concentration (Eloranta, 1999).

The presence or absence of taxa in each system and the averages of the physical and chemical variables were used to build the data matrix. A canonical correspondence analysis (CCA) was performed to detect the relationship among dinoflagellates with all environmental variables. A higher value of the *R* parameter based on canonical weights and structure correlations between the set of variables and species for their respective axes is informed. A Monte Carlo test (499 permutations under the reduced model,  $\alpha = 0.05$ ) was used to find the significance of species' axes and the relationship between species and environment.

Finally, a classification analysis was done based on the Ward minimum variance method (Legendre and Legendre, 1998), the squared Euclidean distance for variables, and the Jaccard similarity index for taxa occurrence (Palacio *et al.*, 2020). The resulting dendrograms are displayed in a single chart including the shared species among aquatic systems. These analyzes were carried out in the CANOCO program for Windows version 4.5 (ter Braak and Smilauer, 2002).

Photographs from a scanning electronic microscope (SEM, JEOL-JSM 6490LV) and differential interference contrast (DIC) microscopy (Eclipse Ni-U, Nikon) were used to make an atlas of the species surveyed (Fig. 2).

#### RESULTS

Twelve dinoflagellate taxa were recorded. The highest species richness occurred at the location Guatapé Reservoir (5 spp), followed by La Fe and Piedras Blancas Reservoirs and Zapatosa Swamp (3 spp); at the remaining sampled sites either two species, or only one species appeared (El Pijiño Swamp and La Ayantuna Lake; Tab. 2). CCA showed that environmental variables explained 53.4% of variance in dinoflagellates, 29.1% along the first, and 24.3% along the second axis.

Three groups of water bodies were clustered according to the occurrence of certain species. The first, the reservoirs, contained *Ceratium furcoides*, *Naiadinium polonicum*, *Parvodinium* cf. *inconspicuum* (Lemmermann) Carty 2008, *Parvodinium elpatiewsky* (Ostenfeld) Kretschmann, Zerdoner & Gottschling 2019, *Peridiniopsis quadridens* (F.Stein) Bourrelly 1968, Peridinium gatunense, P. volzii, and P. willei. Altitude (R = -0.78; ax1), Secchi disk depth (R = -0.55; ax1), pH (R = -0.45; ax1) and oxygen saturation (R = -0.71; ax1) were the variables that contributed most to the spatial arrangement. The second group, the swamps, contained species of *Durinskia* sp. Carty & Elenor R.Cox, 1986, *Glochidinium penardiforme* (Er.Lemmermann)

Locality	Locality	Coordinates	Elevation	Extension	Limnology	References
number			(m)	(km <sup>2</sup> )		
1	El Pijiño	09°19,739' N 74°25,186' W	24	20	Small swamp	
2	El Pozuelo	09°12,806' N 74°29,823' W	23	0.8	Small swamp	
3	Zapatosa	09° 7'58,44" N 73°49'4,91" W	39	360	The largest and main swamp in Colombia, moderate water quality	(Martínez-Silva, 2015; Sánchez <i>et al.</i> , 2015)
4	Ayapel	08° 19' N 75° 6' W	22	106.4	Eutrophic, polymictic, shallow, warm swamp	(Jaramillo-Londoño and Aguirre-Ramírez, 2012; Zabala-Agudelo, 2017)
5	Piedras Blancas	06°17,646' N 75°30,092' W	2,374	0.18	Meso-oligotrophic Reservoir. Its main use is to supply water and generate electrical energy, as well as recreation	(Roldán-Pérez et al., 2001)
6	Guatapé	06°13'20" N 75°10'11" W	1,887.5	62.4	Eutrophic Reservoir. Main use hydroelectric and for tourist, sporting, and fishing production purposes	(Cadavid-González, 2018)
7	La Fe	06° 06' 50" N 75° 30' 15" W	2,100	0.68	Reservoir contaminated with wastewater, crops, and livestock. Main use aqueduct and recreation	(Ramírez Restrepo, 2015)
8	Riogrande II	06°33'-6°28' N 75°32'-75°26' W	2,150	12.14	Reservoir with high turbidity and waters of excellent chemical quality	(Herrera <i>et al.</i> , 2015; López-Muñoz, 2015)
9	Porce II	06°44'57" - 06°48'45" N7 5°09'14" - 75°04'59" W	945	8.90	Hypereutrophic reservoirs. Its purpose is to generate electricity	(Villabona-González et al., 2020)
10	Porce III	06°54,856' N 75°09,879' W	694	4.61	Eutrophic reservoir	(Villabona-González et al., 2020)
11	San Rafael	04° 42'10,2" N 73° 59'14,6" W	2,777	3.71	Reservoir, thermal stratification, low concentrations of Total Phosphorus. Main use aqueduct	(León-López et al., 2012)
12	Chuza	04°34'22,7" N 73° 42'16,8" W	2,990	5.8	Reservoir, chemical stratification, low concentrations of total nitrogen. Main use aqueduct	(León-López et al., 2012)
13	De La Regadera	04°23'4,9"N 74°10'11,9" W	2,997	0.41	Reservoir, chemical stratification, high concentrations of Total Phosphorus and Total Nitrogen. Main use aqueduct	(León-López et al., 2012; Aguirre-Cárdenas et al., 2018)
14	La Ayantuna	02°57'23,5'' N 78°11'29,1'' W	32	3.21*10-3	Small island lake, turbid	(Castro-Herrera et al., 2013)

#### Tab. 1. Limnological characteristics of sampling sites.

Boltovskoy 2000, and *Sphaerodinium fimbriatum* R.H.Thompson 1950 arranged by temperature (R = 0.82; ax1), apparent color (R = 0.93; ax1) and conductivity (R = 0.67; ax1). Finally, the last group, the lake, contained *Parvodinium umbonatum* (F.Stein) Carty 2008 with no variable associated (Fig. 3).

The groups retrieved by the Ward and Jaccard analyses corroborate the CCA associations (Fig. 4). In the Ward analysis, all reservoirs clustered in one group, and the swamps and the lake formed another group. A preliminary classification was possible to establish an order according to the altitudinal range (m of elevation) as follows: lowland systems (0-50 m) comprise all the swamps and the lake; low montane systems (699-947 m) comprise the reservoirs Porce II and Porce III; intermediate montane systems (1,635-2,374 m) comprise La Fe, Guatapé, Piedras Blancas, and Riogrande II Reservoirs; the high montane systems (2,797-3,022 m) include Chuza, San Rafael, and De La Regadera Reservoirs. According to the square Euclidean distance, the most closely related reservoirs were Chuza and San Rafael, De La Regadera and Riogrande II, and Porce II and Porce III. Pozuelo and Pijiño were the most closely related swamps (Fig. 4).

The water systems grouping was similar to the previous analysis according to the Jaccard similarity index's species composition. Based on the dendrogram's topology, seven consistent species were retrieved and displayed in the water bodies as follows: *C. furcoides* occurred in all reservoirs; *P. volzii* occurred exclusively in the high-elevation Chuza and San Rafael Reservoirs; *P. willei* was found in De La Regadera and Riogrande II; *P. gatunense* was found exclusively in Porce II, Porce III, Guatapé, and La Fe; species of *Durinskia* spp. were found



Fig. 1. Geographic location of freshwater bodies assessed.



**Fig. 2.** Atlas of dinoflagellate species surveyed. a) *Ceratium furcoides* (upper right: plates 1' and 4'); b) *Durinskia* sp; c) *Glochidinium penardiforme*; d) *Naiadinium polonicum*; e) *Parvodinium elpatiewski*; f) *Parvodinium inconspicuum*; g) *Parvodinium umbonatum*; h) *Peridiniopsis quadridens*; i) *Peridinium gatunense*; j) *Peridinium volzii*; k) *Peridinium willei*; l) *Sphaerodinium fimbriatum*.

in all the swamps except El Pijiño; *S. fimbriatum* was found only in Ayapel and Zapatosa; *Parv. umbonatum* was found only in La Ayantuna Lake (Fig. 4). The rest of the species occurred in a single aquatic system; those were omitted in the figure.

Guatapé Reservoir hold a uniquely diverse flora composition, while La Ayantuna Lake and Pijiño Swamp had only one species each, *Parv. umbonatum* and *G. penardiforme*, respectively. The most common richness value among all water bodies assessed, regardless of kind, was two. *G. penardiforme* was the most frequent species in lowland swamps, and *C. furcoides* was found in all reservoirs. Both species of *Peridinium* and *C. furcoides* were common in montane systems (Tab. 2).

## DISCUSSION

Worldwide Floristic studies on thecate dinoflagellate ensembles have reported richness from seven to twentytwo species (Ling *et al.*, 1989; Carty, 1993; Borics *et al.*, 2005; Hansen and Flaim, 2007; Cavalcante *et al.*, 2017). This study, despite studying fewer systems (14), yielded evidence for a relative floristic richness (13 spp.) in tropical systems and provides further evidence that the environmental complexity of Colombian systems may influence and generate highly diverse dinoflagellates communities (Donato-Rondon, 2001; Padisák *et al.*, 2016). Similarly, Smith *et al.* (2005) found a positive relationship between phytoplankton species richness and

Locality number	Locality name	Secchi disk depth (m)	Temperature (°C)	рН	Conductivity (µS/cm)	Oxygen saturation (%)	Turbidity (NTU)	Apparent color (Pt-Co)	Species
1	Pijiño	0.87	30.30	6.82	116.09	22.06	15.00	284.11	G. penardiforme
2	Pozuelo	1.42	30.56	7.12	172.80	46.28	17.33	252.67	G. Penardiforme Durinskia sp.
3	Zapatosa	1.17	30.49	6.82	113.88	16.10	15.89	330.56	G. penardiforme S. fimbriatum Durinskia sp.
4	Ayapel	0.48	31.97	7.42	302.00	82.90	18.00	234.67	S. fimbriatum Durinskia sp.
5	Piedras Blancas	1.98	17.51	7.48	53.76	85.38	-	-	C. furcoides Parv. insconspicuum Parv. elpatiewsky
6	Guatapé	4.17	22.94	7.65	40.96	71.94	4.48*	71.78*	C. furcoides N. polonicum Parv. insconspicuum Perid. quadridens P. gatunense
7	La Fe	2.47	19.60	7.01	51.32	73.44	10.60*	51.60*	C. furcoides P. gatunense P. volzii
8	Riogrande II	1.79	20.23	7.68	61.21	83.27	35.70*	-	C. furcoides P. willei
9	Porce III	1.75	25.56	7.09	149.60	76.31	6.25	-	C. furcoides P. gatunense
10	Porce II	1.34	24.74	7.85	175.60	114.53	68.48	-	C. furcoides P. gatunense
11	San Rafael	4.71	16.62	7.11	53.99	80.50	0.22	33.00	C. furcoides P. volzii
12	Chuza	5.07	14.03	7.36	35.22	98.47	0.00	14.33	C. furcoides P. volzii
13	De La Regadera	1.59	15.63	8.79	26.23	114.33	7.22	107.33	C. furcoides P. willei
14	La Ayantuna	0.51	27.45	7.20	101.15	71.75	10	161.00	Parv. umbonatum

Tab. 2. Averages of the environmental variables and species composition in each water body (n=9 in each system).

\*Data taken from Montoya (2007) and Ramírez Restrepo (2015).

the surface area of aquatic system; larger systems contained a higher number of species; this tendency was found in the lakes of the United States (Stomp *et al.*, 2011). The present study has shown that regardless of the type of the system (reservoir, swamp, or lake), the richness of dinoflagellates species was congruent to the size of the water body, Guatapé reservoir and Zapatosa swamp (the largest systems) had the highest species richness, while La Ayanatuna lake (the smallest) had the lowest. However, it is necessary to include more aquatic systems to validate this tendency in tropical aquatic environments.

Regarding variables assessed and considered here as a preliminary robust model by the CCA analysis, it has been demonstrated that the water temperature and electric conductivity of water decreases with altitude while the oxygen saturation percentage increases; all this is explained by a complex interaction of inherent factors - altitude, hydrology and geological origin, among others - (Roldán-Pérez and Ramírez Restrepo, 2008), and this tendency was evidenced in this survey. Lowland systems (all the swamps, the lake, and Porce II and Porce III Reservoirs) showed higher values of temperature, conductivity, apparent color, organic matter concentration, and turbidity. These results agree with those of Roldán-Pérez and Ramírez Restrepo (2008), who recognized elevated turbidity values in tropical systems (swamps and reservoirs) under 1000 m of elevation due to a high degree of lixiviation. However, the dinoflagellate richness values found in these systems were unexpectedly low (1-3 spp), which is contrary to most observations that richness is higher in dystrophic systems (Ling *et al.*, 1989). However, increasing localities to assess and the sampling effort in lowland systems, might reflect more precise biodiversity data.

This survey found dinoflagellate species at all the Andean altitudinal ranges assessed, similarly to Rengefors and Kremp (2018), who stated that dinoflagellates occurred at all alpine altitudinal ranges. The richest values by ensemble (2-5 spp) were evidenced in those systems categorized as intermediate montane systems (Marquez and Guillot 1987, 2001), which correlated with intermediate values of all variables measured and scored intermediate ranges of temperature (17-22°C). High-altitude systems, where richness was relatively low (up to



Fig. 3. Representation of the first and second axes of the canonical correspondence analyses for the 14 studied systems (Environmental variables plotted with  $\lambda > 0.05$ ).

two species), scored low temperatures (14-16°C), high oxygen saturation values, and low values of organic matter. This tendency is in opposition to Ling *et al.* (1989) who proposed that dinoflagellates show preference for high humic acid content. Our findings allow us to hypothesize that intermediate levels of physical and chemical variables positively affect dinoflagellates richness in our tropical Andean systems.

Species composition ensembles formed the same two groups of systems as those in the Jaccard and CCA analyses. In other words, swamps and reservoirs showed distinctive compositions: no species found in swamps was found in reservoirs and vice-versa. This distinction reveals the existence of dinoflagellates spatial structuring

regulated by characteristics of the water bodies. The geographical structuring in our data suggests two distribution types among species: widespread (occurring along the largest distance among reservoirs; 300 km) and restricted (occurring up to 166 km, the largest distance among swamps). These geographical distribution tendencies organisms like phytoplankton in dinoflagellates were previously observed by Padisák et al. (2016) and Rengefors and Kremp (2018) and explained by biogeographical, evolutionary, and macroand microecological aspects (Kim et al., 2004; Cardoso et al., 2010). C. furcoides and species of Peridinium were the species most widespread among the reservoirs. C. furcoides is considered invasive in South America



Fig. 4. Hierarchical clustering of distance and similarity. On the left: Ward minimum variance method and squared Euclidean distance for variables. On the right: Jaccard similarity index for taxa occurrence. In the grey square: clustered species.

(Boltovskoy *et al.*, 2013; Crossetti *et al.*, 2019; Macêdo *et al.*, 2021) and produces blooms in meso- and hypertrophic systems (Bustamante-Gil *et al.*, 2012; Almanza *et al.*, 2016; Jaramillo-Londoño, 2018). *P. gatunense* is widely distributed (Moestrup and Calado, 2018) and also produces blooms in slightly alkaline and warm temperature (23°C) systems (Boltovskoy, 1983). *P. volzii* is found at high altitudes ( $\geq$ 2,600 m), cold temperatures (13-16°C) and slightly acid systems (Hargraves and Víquez, 1981). Finally, *P. willei* is the most extensive worldwide species, found in systems ranging from oligotrophic to eutrophic (Löffler, 1972; Couté and Iltis, 1984; Donato-Rondon, 2001; Boltovskoy, 2003; Cardoso *et al.*, 2010).

Species restricted to reservoirs, like N. polonicum, which has previously been reported in alkaline to neutral, warm (22°C) lakes and oligotrophic to eutrophic systems, produce blooms in eutrophic systems (Roset et al., 2002; Craveiro et al., 2015; Ascencio et al., 2018; Moestrup and Calado, 2018). Perid. quadridens is mostly found in alkaline (pH = 7.5-7.7) and cold systems (Moestrup and Calado, 2018). However, it has been a dominant species in some lakes in the United States during the spring and fall months (Carty, 2014). In the present study, these two taxa were found exclusively in Guatapé Reservoir. Parv. cf. inconspicuum was found exclusively in Guatapé and Piedras Blancas Reservoirs, but it was previously recorded in Colombian high montane lakes (Donato-Rondon, 2001) and in cold, acid, and oligotrophic systems (Boltovskoy, 1999); altitudinal and temperature ranges reported agrees with our results (1600-2300m). the altitudinal (1,600-2,300 m) and temperature range reported agree with our results. Parv. elpatiewsky is a rare species, here found only in Piedras Blancas Reservoir; however, in Europe and South America, it is associated with warm, eutrophic, and neutral to alkaline systems (Ascencio et al., 2015; Moestrup and Calado, 2018).

G. penardiforme, which is broadly distributed among the swamps, was reported to be associated with systems that are neutral to slightly alkaline (pH = 7-8) and warm (15-28°C; Boltovskoy, 1999); this tendency is corroborated here; it also seems to prefer high organic matter content. Species of Durinskia are rare in freshwater systems (Hansen and Flaim, 2007; Cardozo et al., 2010; Yamada et al., 2017), though Durinskia baltica can produce blooms under warm and eutrophic conditions (Lira et al., 2017). Even though the Durinskia specimens collected here were not taxonomically identified to the species level, they yielded the physical variables mentioned above. The more locally distributed swamp species, S. fimbriatum, has been associated with small seasonal lakes in North America (Thompson, 1951), but here it was related to warm, lowland systems with high organic matter content. While Parv. umbonatum is usually

related to warm systems (24-29°C) that range from oligotrophic bromeliad phytotelmata to eutrophic systems (Canosa and Pinilla, 2007; Pinilla *et al.*, 2007; Ramos *et al.*, 2016; Moestrup and Calado, 2018), here it was exclusive to the insular lake. This latter species commonly misidentified as *Parv. inconspicuum* is nowadays clearly distinguished by recent diagnostic morphological characters (Bustamante-Gil *et al.*, 2021). The ecological data here obtained among these two taxa suggest that the best option is to consider them different entities.

This study is the first exploratory and preliminary attempt to understand the ecological aspects that affect Colombian dinoflagellate ensembles. It showed that habitat characteristics of water bodies could be assessed based on physical variables and the distribution of dinoflagellate species could be related to water body types. We argued for the importance of considering an altitudinal gradient among Colombian water bodies to better understand the distribution of dinoflagellates. In future surveys, it will be necessary to include systems from all biogeographical provinces and measure additional variables such as nutrients, hydraulic parameters, along with seasonality to further characterize their influence on the ecological dynamics of dinoflagellates in tropical aquatic environments.

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