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ORIGINAL ARTICLE

Effects of the hydrological cycle on the phycoperiphyton assemblage in an Andean foothill stream in Colombia

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ABSTRACT

The Guarinó River is a torrential system that is located in the foothills of the Colombian central Andean mountains that naturally experiences severe hydrological disturbances, which were higher during the Niño-Niña/Southern Oscillation (ENSO) between 2007 and 2010. The seasonal and interannual variabilities in the taxonomic composition, richness and density of phycoperiphyton assemblages (ecological descriptors) from the Guarinó River were examined in relation to the physical and chemical environmental changes associated with the hydrological cycle between 2007 and 2010. The values of the ecological descriptors and environmental variables were analyzed via ANOVA, ANCOVA and Canonical Discriminant Analysis to establish temporal patterns and relationships between the variables. Eighty-seven taxa belonging to Cyanobacteria, Chlorophyta, Charophyta, Ochrophyta, Cryptophyta, Euglenozoa and Dinophyta were identified. Flow, water temperature and dissolved oxygen corresponded with the hydroclimatic variation and allowed for the differentiation of the El Niño and La Niña periods. Phycoperiphyton density differences matched the environmental variation pattern with a significant annual increase in the number of individuals during El Niño, whereas annual differences related to richness were not evident. The replacement of genera according to their drag or desiccation tolerance and the persistence of genera tolerant to high hydrological disturbances, such as Fragilaria*,* Nitzschia*,* Gomphonema*,* Navicula *and especially* Lyngbya*, was observed.*

Key words: Flow; seasonality; climatic alterations; disturbance.

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INTRODUCTION

Periphytic algae or phycoperiphyton, according to Foerster and Schlichting (1965), Vettorato *et al*. (2010), Lange *et al*. (2011), Wu *et al*. (2009), are assemblages of organism that are responsible for primary production in lotic aquatic ecosystems and are a direct trophic source for many macroinvertebrates and fish. They are the main autochthonous source of energy in some tropical forested headwater streams (Mantel *et al*., 2004; Lau *et al*., 2008, 2009; Li and Dudgeon, 2008) and are more important than allochthonous organic matter for consumers in this system, mainly during the dry season. (March and Pringle, 2003; Salas and Dudgeon, 2003). The establishment, composition and growth of this assemblage is influenced by many factors, such as nutrients and light availability, grazing, physical disturbance, temperature and chemical variables.

Flow is an environmental attribute that affects the algal composition of the assemblage and the richness and density in rivers (Biggs and Hickey, 1994; Passy, 2001, 2007). It is the major mechanical force in running water and has both positive and negative effects on periphyton (Passy and Larson, 2011). Changes in the hydrological regime in rivers affects the physical and biological environments, constituting one of the most serious threats to the biotic integrity of systems because such changes affect habitat structure and the functional aspects of the environment (Agostinho *et al*, 2004; Goldsborough and Robinson, 1996). The availability of substrata for phycoperiphyton in the riverbed is seriously affected by the hydrological regime, and an increase in flow velocity acts as a stressor causing the dragging and/or drifting of phycoperiphyton downstream and as a selection pressure for those genera that can serve as pioneers (Gari and Corigliano, 2004). Spatial and temporal variations of the density and dominance of genera respond to hydrological variability as a function of its incidence on the dispersion processes, establishment and persistence (Reynolds, 1993)

Tropical streams in the Andean foothills experience slight variations in water temperature throughout the year because of a minor effect from the thaw, but experience large variations in flow because of seasonal changes in rainfall. Rainy periods that produce high water flow alternate with drier periods that are characterized by basal flow (Donato *et al*., 2014). During the rainy period, water flow may be irregular (Rivera and Donato, 2008) and episodic spates can occur. The intensity of spates during the rainy period is associated with the rainfall frequency and local topography; it may affect streambed stability, turbidity and the mobility of the substrata (Jacobsen, 2005, 2008). Such hydrological variability is associated with changes in factors involved with the flow, such as the water speed and depth, and constitutes a disturbance that triggers changes in the phycoperiphyton assemblage and its succession due to their small size, passive dispersal method and generally limited mobility (Connell, 1978; Townsend, 1989; Winemiller *et al*., 2010, Passy, 2007; Algarte *et al*., 2014). However, the phycoperiphyton is probably the assemblage that is most resilient to variations in flow because it responds very rapidly to environmental changes due to its short life cycle (days), high reproduction rate and adaptations or forms of attachment to the substrata in many genera that affect the drifting velocity (Biolo and Rodrigues, 2013).

It is difficult to generalize the dynamics of phycoperiphyton in lotic systems because there is a disparity among the results concerning the influence of hydrological conditions on the algal density and richness in rivers in different regions. The variability in the hydrologic cycle depends on geomorphological and regional weather characteristics and on global events that have a significant effect on the rainfall and drought regime, such as the El Niño - La Niña/Southern Oscillation phenomena (ENSO). These phenomena affect habitat conditions, such as substrata availability, which can be covered by particulate matter or remain emergent, obstructing colonization; flow velocity, which causes subsequent drifting; or water turbidity, which affects the photosynthetic rate (Biggs and Smith, 2002).

The effects of the Niño-Niña/Southern Oscillation ENSO phenomenon on the regional hydrologic conditions in South America are strong, but its effect on freshwater ecosystems remains poorly studied (Blanco, 2003). Reports about the influence of climatic changes on freshwater algal assemblages have focused on planktonic assemblages in temperate lakes and on the occurrence of algal blooms associated with their stratification (Elliott *et al.*, 2005; Mackay *et al*., 2006). However, few studies regarding the effect on phycoperiphyton have been performed in lotic systems, where changes in precipitation and stream flow are not critical for stratification (Viney *et al*., 2007). Young and Huryn (1996) conducted the first study in a stream system, the Taieri River (Canada), where they found the predominance of autotrophic communities during an El Niño low-flow year. Studies by Biggs and Smith (2002) and Biggs *et al*. (2005) in New Zealand rivers found that when flow and its associated drag-disturbance process is low for prolonged periods of time, some streams that are normally dominated by diatoms and cyanobacteria can become dominated by a higher biomass of green filamentous algae. In Andean rivers, where the ENSO phenomena induce changes in precipitation affecting stream hydrology, a similar pattern of the phycoperiphyton response is expected.

Some studies on phycoperiphyton assemblages in tropical high mountain rivers have been conducted in Colombia to evaluate the effect of environmental variables (Ramírez and Viña, 1998; Montoya-Moreno, 1998; Martínez and Donato, 2003; Rivera-Rondón and Díaz-Quirós, 2004; Zapata and Donato, 2005; Pedraza and Donato, 2011; Hernández-Atilano *et al*., 2005; Valenzuela *et al*, 2006; Zapata and Donato, 2008; Rivera-Rondon and Donato, 2008; Bustamante *et al*., 2008; Marín-Villegas *et al*., 2011). Some of these authors agreed that weather and hydrological variables determine the growth and stability of the algal assemblages in those systems. Others found a different behavior, so a variety of explanations exist according to the function of a community successional stage, system disturbance regime and substratal stability (Biggs and Smith, 2002). No studies on these issues have been performed in the rivers of the Andean foothills. Rivers with high flow variations, such as those located in the Andean foothills, have a high phycoperiphytic taxonomic richness; they are especially interesting to study because of the influence of the physical and chemical variables associated with the hydrological cycle on this algal assemblage. Such is the case for the Guarinó River, a torrential system located in the Colombian Central Andes that displays a high algal richness considering that it is a highly disturbed habitat (Biggs, 1996; Peterson, 1996). This river system showed significant environmental variation during the period 2007-2010, which is associated with its torrential regime and ENSO phenomena.

The goals of this study were: i) to characterize the temporal variations (seasonal and interannual) in the phycoperiphyton assemblage structure (richness and density); ii) to evaluate the relationships between the temporal patterns of the phycoperiphyton assemblage and the hydrological cycle environmental parameters during the El Niño/La Niña-Southern Oscillation (ENSO) phenomena from 2007 to 2010. Considering some of the particular characteristics of Guarinó River, such as the high hydrological disturbance regime, it is our hypothesis that the phycoperiphytic assemblage shows seasonal and interannual patterns of variability in composition, density and specific degree of dominance as a response to the local hydrological regime, favouring resilience or resistance to extreme events. In this way, this study contributes to the understanding of the patterns and processes related to the phycoperiphyton assemblage from the Andean torrential foothills rivers under extreme hydrological conditions.

METHODS

Study site

The Guarinó River is a third-order stream in the Los Nevados Natural Park. It is located in the foothills of the Colombian central mountain range and is a direct affluent of the Magdalena River (Fig. 1). The prevalent life zone is tropical rain forest (Holdridge, 1982), and it has a wide valley with rainfall regime higher than 3800 mm, a temperature higher than 25°C and a relative humidity ranging from 60 to 80%. The hydrological regime is bimodal, with two dry periods (February and August) and two rainy periods (April and October). The main channel is 98 km long until the confluence of the Magdalena River, and a rapid transition between the high zone and the alluvial plain (last 16 km) is evident, with periodic flooding events (Ríos-Pulgarín *et al*., 2015).

Experimental design

The experimental design and environmental variables as well as the method of measurement corresponds to the study of Ríos-Pulgarín *et al*. (2015) , which was developed simultaneously. Three sampling areas were located on the alluvial plain (foothills) of the Guarinó River, [Jardín (north 5° 17’ 41.4” and west 74° 52’ 25.2”); area 2: Bocatoma acueducto (north 5° 18’ 30.5” and west 74° 51’ 31.0”); and area 3: Casanguillas (north 5° 19’ 07.9” and west 74° 49’ 37.7”)]. All of the areas had a similar level of anthropogenic impact, vegetation cover and habitat characteristics, such as the margins constituted of substrates containing stones and streambeds containing sand and cobbles. These areas were between 293 and 375 meters in altitude and were separated by two km. Four field trips were made between August 2007 and April 2010 to the three sampling stations every three months; two of these field trips occurred during the dry season (August and February) and two during the rainy season (October and April). These periods were established according to historical records containing 30 years of precipitation data from the weather station Puente Victoria located in area 1, belonging to the Instituto de Hidrología, Meteorología y Estudios Ambien-

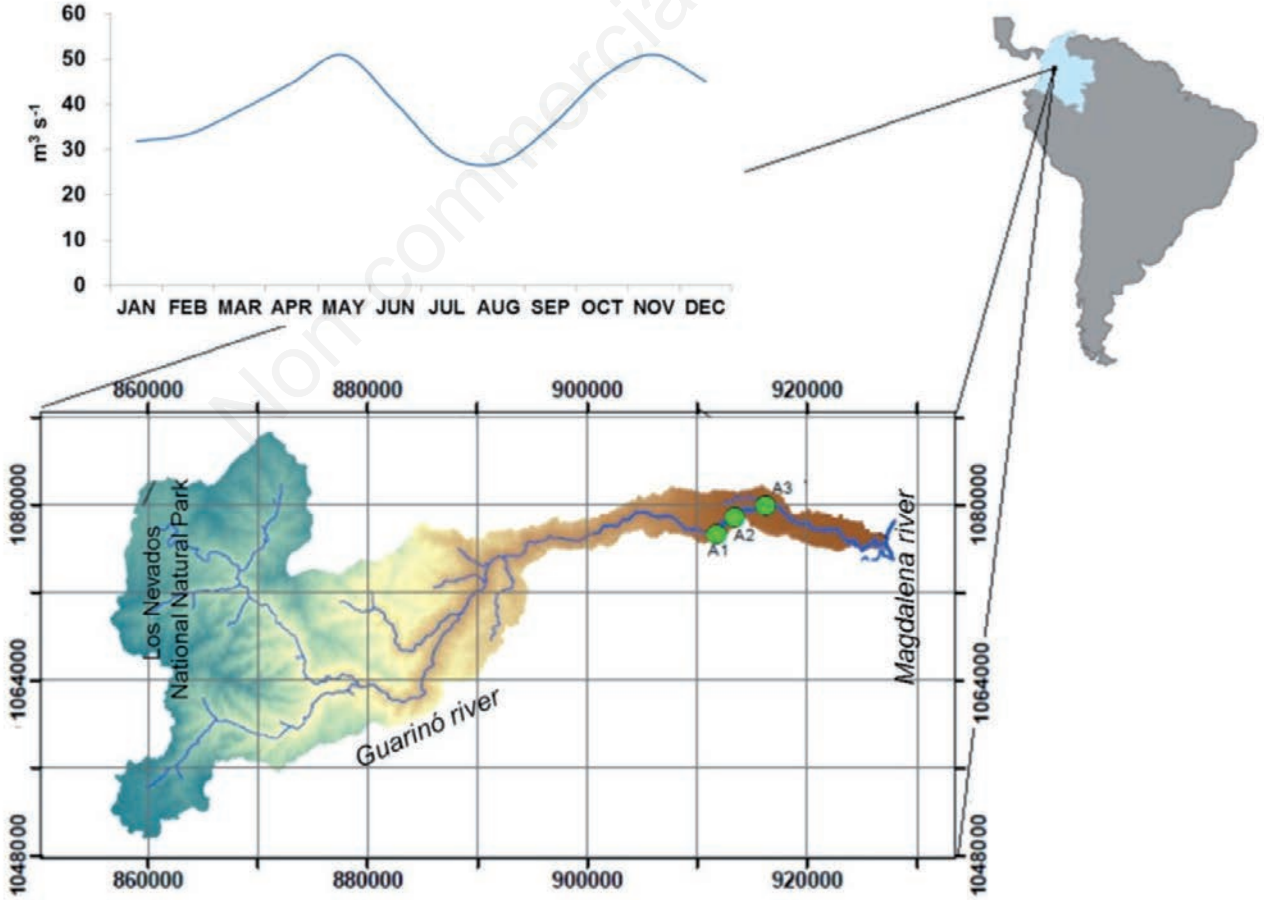

Fig. 1. Geographical location of the region of study and sampling stations: A1) Jardín, A2) Bocatoma acueducto, and A3) Casanguillas in the Guarinó river and the average flow rate between 1980 and 2010. Source: Ríos-Pulgarín *et al*., 2015.

tales de Colombia - IDEAM (2012) (Fig. 1). Both the level and flow values obtained from IDEAM for area 1 were validated and adjusted by gauging (by the profile cross section method and a current meter) in each area.

Conditions associated with El Niño-Niña/Southern Oscillation (ENSO) were defined according to the criteria of Ríos-Pulgarín *et al.* (2015) , which was based on a report by ONI (Oceanic Niño Index) from NOAA-NCEP (2014) for the American Pacific and comparisons between the monthly historical mean rainfall and river flow in the catchment basin and observed during the sampling periods. Based on this information, the period 2007-2008 (year 1) was defined as a transition to the La Niña phenomenon (early phase), 2008-2009 (year 2) as a La Niña year and 2009-2010 (year 3) as an El Niño year (NOAA-NCEP, 2012, 2014; IDEAM, 2012).

Environmental variables

All of the environmental parameters correspond to the study by Rios-Pulgarín *et al.* (2015). During each period and at each sampling station, *in situ* variables, such as dissolved oxygen (mg L^{-1}), conductivity (ms cm^{-2}), pH and water temperature (°C), were measured using Shott and Mettler Toledo cells and water samples were analyzed in the laboratory for turbidity and nutrients, such as orthophosphates and total nitrogen (mg L^{-1}). All of these variables were analyzed according to Standard Methods (APHA, 2005). Information on the Hydrologic variables, such as the river flow (m^3s^{-1}) and rainfall (mm), were supplied by IDEAM (weather station Puente Victoria) and ISAGEN (Energy Generating Company of Colombia).

Algal assemblage

Phycoperiphyton sampling was conducted along the river shore in each area in 10 randomly collected substrates composed of stones, which were immersed in the riverbed over a 100 m^2 transect. The material that was attached to the substrates was removed with plastic tooth brushes from a quadrant with an area of 10 cm^2, so a final area of 100 cm^2 per station was sampled. The collected samples were preserved with 10% lugol and kept in the dark until laboratory analysis. Each sample was homogenized by manual shaking, and a subsample of 1.0 mL was taken. For qualitative and quantitative analyses, a Kolwitz chamber and an inverted microscope was used with a magnification of 400x on 30 random fields as recommended by Bicudo (1990). A taxonomic determination was performed at the genera level using the keys and illustrations of Prescott (1962), Bicudo and Bicudo (1970), González (1988), Cox (1996), Ramírez (2000), Menezes and Días (2001), Andries (2005) and Bicudo and Menezes (2008). Counting was performed until the most abundant genera had reached 300 individuals. The results are expressed per unit area (ind m^{-2}). Genera were classified according to their form of attachment or strategy of adhesion to the substrates, which were previously established by studies on the phycoperiphyton growth morphology (Martinez and Donato, 2003; Sala *et al*. 2008, Peterson and Hoagland, 1990; Tuchman and Stevenson, 1991; Kutka and Richards, 1996; Passy, 2007; Kutka and Richards, 1996; Rimet and Bouchez, 2012; Kutka and Richards, 1996; Biggs, 1996; Andramunio-Acero, 2013; Algarte *et al*., 2014), including the prostrate, pedunculated, filamentous, erect and ticoepiphyte habits. A prostrate habit describes genera that grow attached to a substrate by their entire valve surface; they are often found in the base of algal mats. Genera that have an erect growth form are apically attached, but perpendicular to the substrate; they are usually solitary. Pedunculated genera produce a stalk that adheres to the substrate. Filamentous genera are diatoms that form chains or other groups, such as several genera of Charophyta and Chlorophyta. Ticoepiphyte is a status that is assigned to genera whose presence in phycoperiphyton could be considered accidental.

Data analysis

To establish the variability of the biotic and abiotic variables between years and seasons, the areas were considered to be replicates because the areas are located on the same stretch of river (floodplain) and have similar habitat conditions. To establish the seasonal and annual variability for the environmental variables of the Guarinó River between 2007 and 2010, analysis of variance (ANOVA) was used after verifying the assumptions of normality (Kolmogorov-Smirnov test) and variance homogeneity (Levene's Test). According to a proposal by Ríos-Pulgarín *et al*. (2015), ANOVAs were conducted to evaluate the effect of the year and hydrological period (factors) on the dependent environmental variables, including dissolved oxygen, conductivity, pH, water temperature, turbidity, total nitrogen, orthophosphates, DBO, river flow and rainfall. The procedure included *post hoc* comparisons that were evaluated using Tukey's test to determine the levels that differed for each factor (Quinn and Keough, 2002). Annual patterns of the environmental variables were tested via Canonical Discriminant Analysis (CDA) on the parameters that showed greater variability. In CDA, a variable is represented as a vector whose length and direction is proportional to its contribution to explain the variance (Guisande, 2015). The result establishes whether the variable considered differentiates the sampling years, and the first discriminant axis expresses the percentage of variability explained by the variables; it also allows for the study of the effect of different explanatory variables on the classification obtained.

Analysis of covariance (ANCOVA) was used to evaluate the effect of the year and hydrological period as well as its interaction with the algal assemblage structure (genera richness and density). The variables year and period were considered to be categorical variables (factors), and river flow was considered to be a covariable. Levene's Test for Homogeneity of Variance and Lilliefors (Kolmogorov-Smirnov) normality test were performed. A homogeneity of slopes test for multiple regression between each variable and the river flow in each factor (year and season) was performed.

The temporal patterns (differences between years) of the algal assemblage composition and its relationships with the environmental variables were tested *via* Canonical Discriminant Analysis (CDA), which was conducted on density data for the most frequent genera, excluding those that were uncorrelated and that had less than 5% frequency and 3% abundance (Gauch, 1982; Blanco, 2003). CDA for temporal patterns of algal divisions and habits were also applied. Contributions of genera, divisions, habits (life forms) and the environmental variables were shown in graphical representation as vectors, the length of which is proportional to the contribution of each variable to the explanation of the variance for the first canonical axis. All analyses were conducted in R Software vers. 2.15.2 (2012) and RWizar (Guisande, 2015).

RESULTS

Environmental variables

Rainfall and flow values showed differences between 2007 and 2010 in the Guarinó River. During the first year (2007-2008), a clear seasonality was observed, with distinct periods of rain and drought. During the second year (2008-2009) seasonality decreased, as indicated by a decrease in the magnitude of the rainfall and especially by drought, but rains were persistent throughout the year. During the third year (2009-2010), seasonal rainfall was observed, but the amount was very low, favouring the persistence of low flows (Fig. 2).

Physical and chemical variables showed seasonal variations (Tab. 1), but were higher for flow, oxygen, temperature and turbidity. All of the variables showed significant differences between years ($P<0.05$), except alkalinity. The *post-hoc* comparisons detected differences for year 3 (El Niño) in temperature, pH, conductivity, dissolved oxygen and flow, whereas the values of turbidity, DBO, STT and nitrogen differed during year 2 and hardness and orthophosphate during year 1.

Canonical Discriminant Analysis applied to environmental variables discriminated between years with 90.7% for the first canonical axis (Fig. 3), and three different groups were distinguished. The first group included samples that were taken during year 3 corresponding to the El Niño/Southern Oscillation phenomena-ENSO that was associated with higher values of temperature, pH, conductiv-

Tab. 1. Average values of the physicochemical variables measured in the Guarinó River between 2007 and 2010. This table is modified from Ríos-Pulgarín *et al.* (2015).

Environmental variables	Year 1 (La Niña early phase)				Year 2 (La Niña mature phase)				Year 3 (El Niño)				ANOVA		*Post-hoc* comparisons	
	Dry1 (Aug07)	Rainy1 (Oct07)	Dry2 (Feb08)	Rainy2 (Apr08)	Dry1 (Aug08)	Rainy1 (Oct08)	Dry2 (Feb09)	Rainy2 (Apr09)	Dry1 (Aug09)	Rainy1 (Oct09)	Dry2 (Feb10)	Rainy2 (Apr10)	F	P		
Temperature (°C)	23.50	21.67	22.30	21.67	21.47	21.77	21.30	22.27	23.53	24.87	24.13	24.77	15.20	0.00020	Y1 Y2	Y3
pH	7.95	7.10	7.25	6.71	7.02	6.77	7.70	7.87	8.11	7.64	7.80	7.81	6.50	0.004	Y1 Y2	Y3
Conductivity (μScm^{-2})	94.47	58.13	80.00	63.80	84.50	62.10	70.83	68.43	87.55	112.60	93.60	81.70	7.31	0.0023	Y1 Y2	Y3
OD (mgL^{-1})	8.46	8.00	8.10	7.59	7.90	8.96	8.60	8.05	9.63	6.00	6.07	6.03	8.50	0.001	Y1 Y2	Y3
DQO (mgL^{-1})	43.00	50.33	12.33	64.33	981.67	823.33	58.67	32.00	48.33	48.00	81.00	129.33	3.74	0.034	Y1Y3	Y2
STT (mgL^{-1})	158.67	396.11	304.33	563.00	8966.67	2170.00	398.67	368.33	487.00	136.33	108.33	106.33	12.87	0.00073	Y1Y3	Y2
Alkalinity (mg CaCO$_3$L^{-1})	50.83	32.50	40.00	36.67	31.67	39.67	45.33	39.00	38.67	41.00	31.67	58.33	0.164	0.84	Y1 Y2	Y3
Hardness (mg CaCO$_3$L^{-1})	50.00	30.00	28.67	26.67	85.00	48.33	31.33	42.00	41.33	71.33	48.00	74.00	8.12	0.001	Y1 Y2	Y3
Total Nitrogen (mgL^{-1})	3.52	1.41	3.80	4.50	20.77	15.63	3.13	2.50	2.63	1.05	1.58	1.24	13.58	0.00004	Y1Y3	Y2
Turbidity (NTU)	21.33	153.33	45.00	112.33	5300.00	1806.67	135.67	190.00	155.33	33.00	21.33	22.67	18.22	0.00004	Y1Y3	Y2
Orthophosphates (mgL^{-1})	1.70	0.62	0.53	0.98	4.40	0.23	0.06	0.05	0.34	0.10	0.16	0.41	5.61	0.007	Y1 Y2	Y3
Average depth (m)	0.94	1.45	1.13	1.25	1.03	1.15	1.20	1.45	0.81	0.62	0.65	1.14	19.78	0.00006	Y1 Y2	Y3
Flow (ms^{-1})	49.66	68.50	50.05	34.97	53.29	57.17	53.69	80.25	50.85	46.95	17.02	30.32	9.74	0.00047	Y1 Y2	Y3

Differences between years were determined by Tukey post-hoc *comparisons (underline indicates homogeneous group). Y1, year 1; Y2, year 2; Y3, year 3.*

ity and hardness. The second comprised those samples with the highest flow values for oxygen, river flow, DQO, total nitrogen, total iron, turbidity and STT during a La Niña mature phase (year 2), and the third group was composed of samples taken in year 1 (a La Niña early phase), corresponding to high rainfall values, but intermediate conditions were noted for most of the variables considered.

Seasonal variation in the algal assemblage

Eighty seven taxa belonging to Cyanobacteria, Chlorophyta, Charophyta, Ochrophyta, Cryptophyta, Euglenozoa and Dinophyta were identified; these taxa reached a total density of 48882.31 ind. m^{-2}. Considering the number of taxa per division, Ochrophyta was predominant with 32 taxa (36.7% of the total) and diatoms were particularly abundant (Bacillariophyceae class) in this group; *Navicula, Fragilaria, Melosira* were the most abundant genera; green algae (Chlorophyta and Charophyta) were represented by 29 taxa (33.3%), Cyanobacteria had 17 taxa (19.5%), Euglenozoa six (6.89%), Dinophyta had two (2.29%) and Cryptophyta had one (1.14%). Fig. 4 shows the temporal distribution of the different division densities. During year 1 (La Niña early

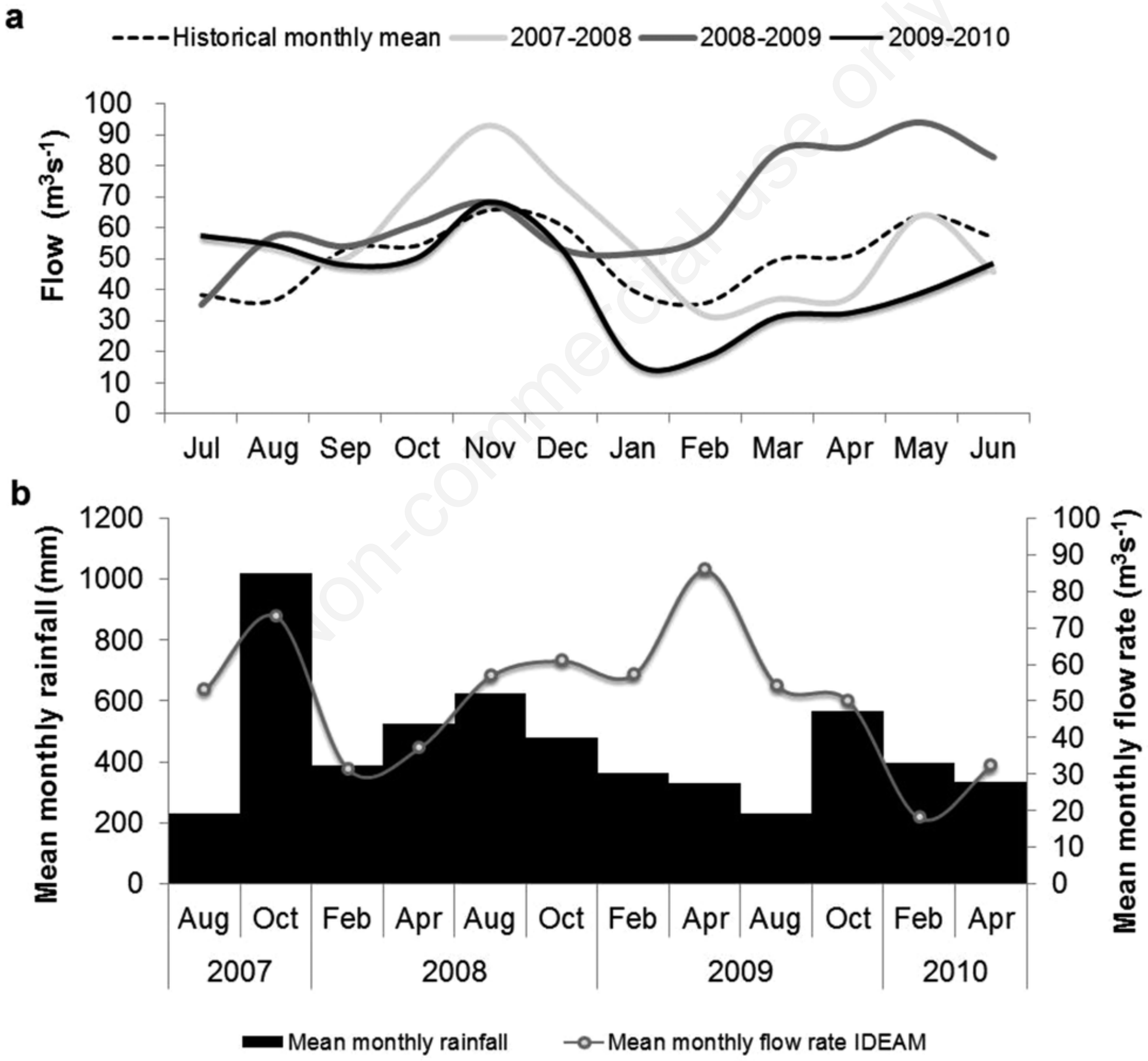

Fig. 2. Hydrological regime of the Guarinó River; a) flow during the cycle 2007-2008 (year 1), 2008-2009 (year 2), and 2009-2010 (year 3), with respect to the average flow rate between 1980 and 2010. b) Average values of rainfall and flow between 2007 and 2010. Source: Ríos-Pulgarín *et al.*, 2015.

phase), Ochrophyta contributed to almost 50% of the density in February, April and August, whereas in October, it decreased significantly to 25% and Cyanophyta increased, with a contribution of 65%. In the second year (La Niña mature phase), the density of Ochrophyta declined, as did that of all of the groups in general, except for Cyanobacteria, contribution of which increased. During the third year (El Niño year), Chlorophyta and specially Ochrophyta increased. The genera that had the highest densities were *Lyngbya* (15.95%), *Navicula* (12.93%), *Fragilaria* (12.46%), *Melosira* (10.66%), *Chroococcus* (9.42%), *Oscillatoria* (4.85%), *Nitzschia* (4.75%) *Chlorococcum* (3.18%) *Gomphonema* (2.84%) and *Cymbella* (2.81%), as is shown in Supplementary Tab. 1, so the cumulative density for these taxa was 80.54%.

During the early and mature phase of the La Niña and El Niño years, some differences related to the contribution of algal divisions and habit by year were observed. Algal divisions were different in the third year (El Niño), explaining 74.1% of the variance, and the algal habits were different, explaining 60.1% of the variance (Fig. 5). The driest periods of El Niño in the river were characterized by a greater density of green algae (Chlorophyta and Charophyta) and diatoms (Ochrophyta). This period was also characterized by a greater density for all of the habits, except ticoepiphytic, which occurred only during the early La Niña phase. Although the third year contained the highest diversity of algal forms of attachment (filamentous, erect and pedunculated), the increase in the variance during this period came mainly from the prostrate growth form.

Density did not show a seasonal pattern; the highest values occurred in August 2007 and February and April 2010, which were influenced by the dry season (Fig. 6). During the last two sampling periods, the highest taxonomic richness also occurred, showing a pattern or tendency of genera richness to increase in the dry season throughout the study or during the transitional phases to these seasons. It was not possible to establish defined seasonal trends among the most abundant and frequent genera, so the high abundance of *Lyngbya, Chlorococcum* and *Gomphonema* in the dry season and *Oscillatoria* in the wet season were the only recognizable trends (Fig. 7). However, annual differences, such as the decline of *Chroococcus* and *Oscillatoria* densities and an increase of *Melosira, Lyngbya, Nitzschia, Chlorococcum, Gomphonema* and *Cymbella* densities during the third year of the study (El Niño), were evident.

The values of algal density showed significant seasonal and interannual mean differences (P=0.006 and 0.001, respectively), whereas richness showed very significant differences among years (P=0.0005), but did not show seasonal differences (Tab. 2). the flow values were not related to richness or density differences (P>0.5). The richness values were higher during the third year (corresponding to El Niño-Southern Oscillation, ENSO), but were similar during the dry and wet seasons, especially in the second and third year. Density was higher in the third year and was higher during the first dry season of each year (Fig. 6).

Relationship between assemblage and environment

The CDA for the phycoperiphyton density data showed interannual differences, with a cumulative variance of 87.4% for the first canonical axis. The genera showed temporal variations related to annual environmental gradients, so it was possible to differentiate the driest period of Niño-Southern Oscillation, ENSO during the third year (Fig. 8). Differences in the phycoperiphyton densities were caused by *Chlorococcum*, *Cymbella, Gomphonema, Achnanthes,* and *Cylindrocystis* and, to a lesser degree, by *Nitzschia, Navicula, Fragilaria, Chaetophora* and *Cyclotella*, which were associated with higher values of temperature, conductivity and pH during the third year, whereas *Chroococcus, Gyrosigma, Anabaena* and *Trachelomonas* were associated positively with turbidity and orthophosphate during the first year. The genera did not contribute to differentiate in the second year (La Niña), which was characterized by maximum values of the flow level, nitrogen and dissolved oxygen.

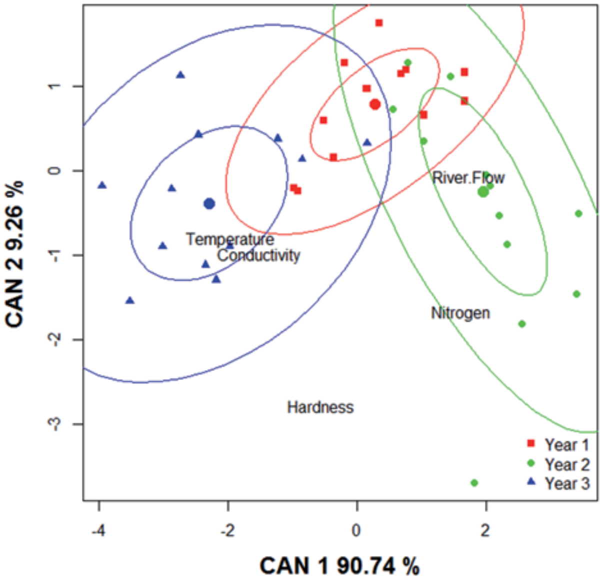

Fig. 3. Biplot of the discriminant analysis of the environmental variables between August 2007 and April 2008 (Year 1-La Niña early phase), August 2008 and April 2009 (Year 2-La Niña mature phase) and August 2009 and April 2010 (Year 3-El Niño). The ellipses show the significance levels of 0.5 (inner ellipse) and 0.95 (external ellipse) of each year. Source: Ríos-Pulgarín *et al.*, 2015.

DISCUSSION

During the ENSO events from 2007 to 2010, the ecosystem of the Guarinó River displayed hydrological *homogenization* associated with sustained high flow during La Niña (year 2) and low flow during El Niño (year 3). Year 1 (the early phase of La Niña) was a transitional period with marked seasonality and intermediate levels of most of the environmental variables and therefore was a reference for system conditions in the absence of ENSO events. In fact, although NOAA considers the second half of 2007 as part of La Niña phenomena, only in years 2 and 3 did the hydrological variability fall outside of the natural range of variability observed in the basin, which shows local differences in the effect of this phenomenon that were probably dependent on factors such as topography, vegetation cover and land use. So our study emphasizes that the effects of global scale phenomena must be evaluated locally, avoiding generalizations.

Associated with high flows, La Niña increased the turbidity, nutrients and oxygen, while low flows during El Niño increased the temperature, conductivity and pH. These results agree with the results reported by Blanco (2003) for an Andean river during ENSO Phenomena in 1997-1999. However, it was additionally found that, notwithstanding that August 2009 is listed as part of El Niño, local hydrological characteristics displayed the effects of an antecedent La Niña because the high flow caused water accumulation in the basin, delaying drought. This suggests a modulating effect of the local geomorphology on the dynamics of the ENSO phenomenon and is consistent with the results of studies by Moles and Dahm (1990) and Scarsbrook (2003).

Regarding the phycoperiphyton assemblage, in torrential systems, such as the Guarinó River, different growth forms or patterns of attachment to the substrates allowed a greater number of genera to remain attached during seasons that experienced hydrological disturbances. Water level

Tab. 2. Summary of the ANCOVA results for the algal density and richness in the Guarinó River between 2007 and 2010.

Dependent variable	Trans	Factor	Variable	F value	df	P	*Post-hoc* comparisons
Species number	Natural logarithm (LN)	Flow (m^3 sec^{-1})	Covariable	0.06	1	0.8	
		Year	Factor 1	10.64	2	0.0005***	Y1Y2 Y3
		Season	Factor 2	1.94	3	0.15	
Density (ind m^{-2})	Natural logarithm (LN)	Flow (m^3 sec^{-1})	Covariate	0.34	1	0.56	
		Year	Factor 1	8.47	2	0.001**	Y1Y3 Y2
		Season	Factor 2	5.19	3	0.006**	R1 R2 D1 D2

Differences between years were determined by Tukey post-hoc *comparisons (underline indicates homogeneous group); Y1, year 1; Y2, year 2; Y3, year 3; D1, dry 1; D2, dry 2; R1, rainy 1; R2, rainy 2. ***0; **0.001.*

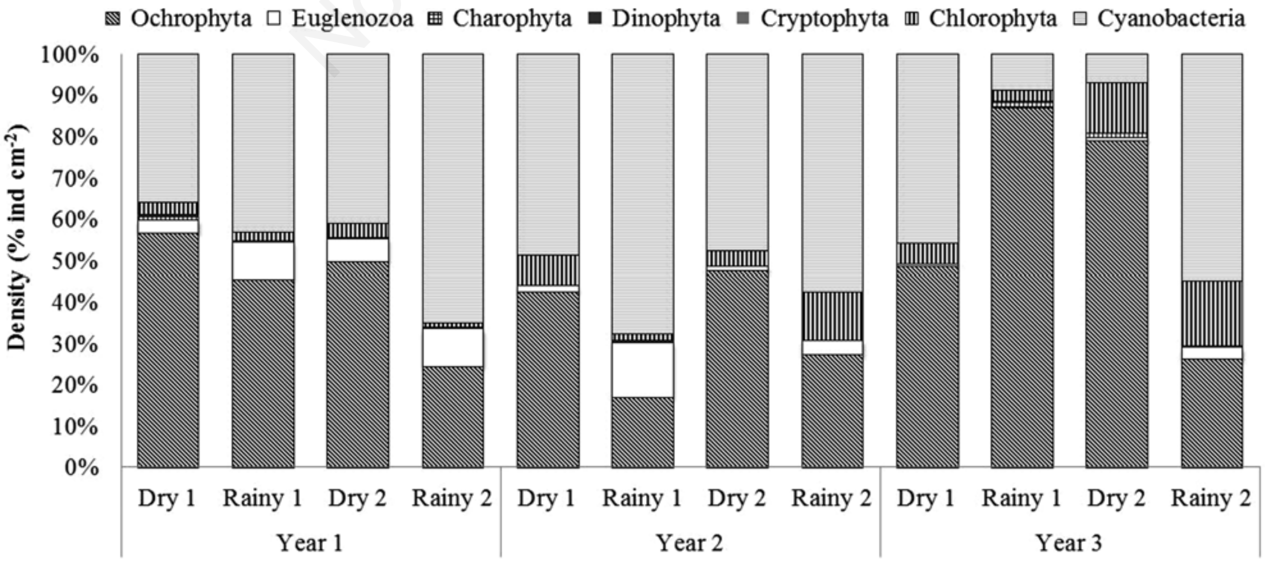

Fig. 4. Percentage of the density of the different groups of phycoperiphyton in the Guarinó River from 2007 to 2010.

fluctuations and a large movement of the water column affected the substrates and maintained the assemblage in early stages of development. Therefore, prostrate genera, such as *Achnanthes* and *Cocconeis*, or erect genera, such as *Navicula*, were the most abundant. Their form of attachment consists of a valve whose surface adheres entirely to the substrate (*e.g.*, *Achnanthes* and *Cocconeis*) (Passy, 2007) and of an elongated morphology with the presence of raphe (*e.g.*, *Navicula*). These forms of attachment facilitate adherence to the substrate in spite of flow fluctuations (Stevenson *et al*., 1996; de Nicola, 2000; Raunio and Soininen, 2007; Wunsam *et al*, 2002). Donato-Rondón (2008) stated in their study of an Andean high gradient river that, during high flow periods, flattened or prostrate shaped (ovoid and oblique) algae dominated because their morphology favoured ecological performance and fitness; these shapes were not very sensitive to the hydrological disturbance and to the morphological conditions of the substrate. According to Biggs (1996), small and prostrate diatoms, such as *Cocconeis* and *Achnanthes*, precede some erect and stalked diatoms, such as *Navicula* and filamentous green algal colonization, allowing the formation of a three dimen-

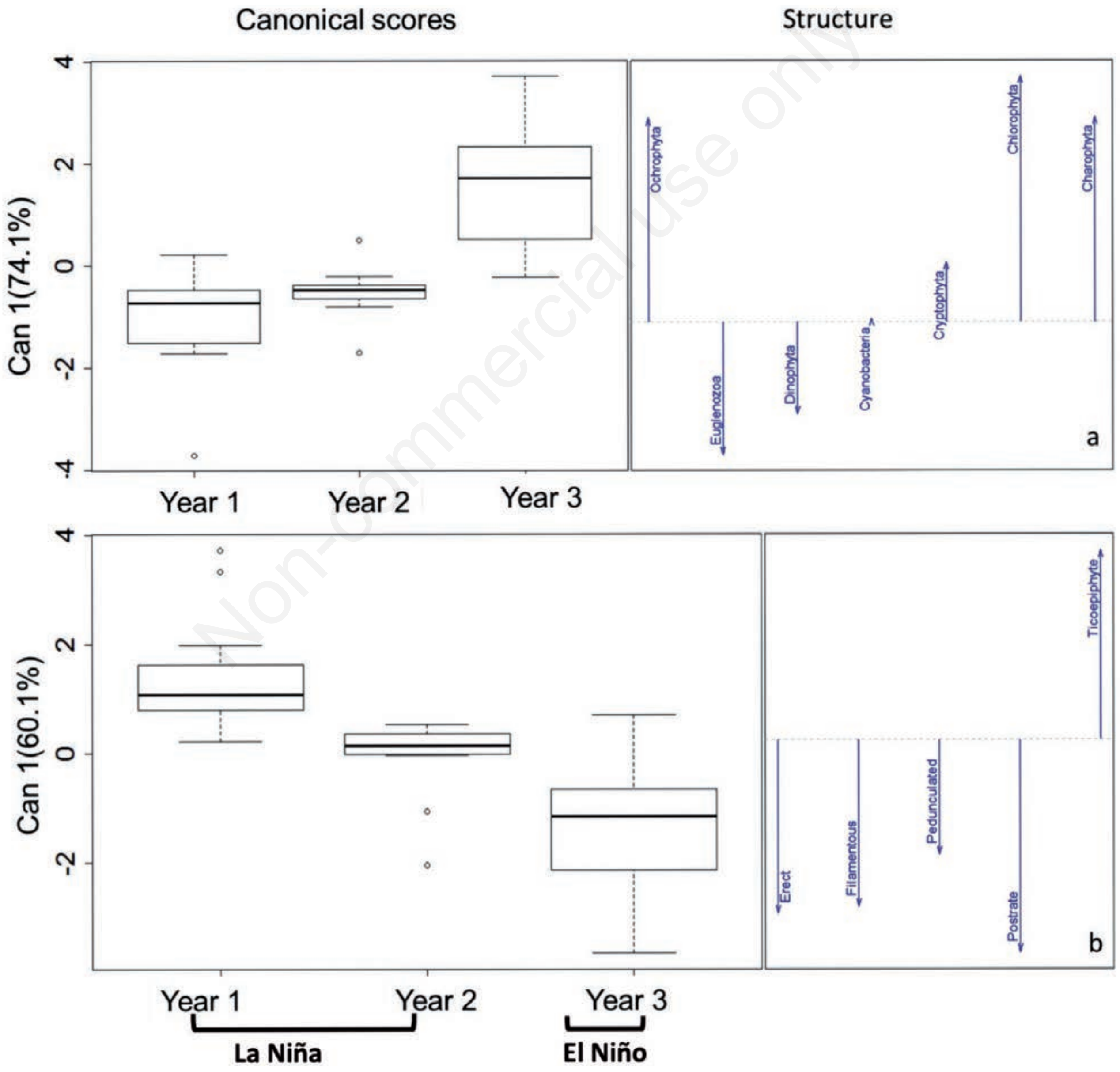

Fig. 5. Canonical Discriminant Analysis for algal divisions (a) and habits (b) of the Guarinó River during the events of the ENSO that occurred between 2007 and 2010.

sional mat. Once *Cocconeis* and *Achnanthes* have attached to the substrate, they can reproduce very rapidly and form a layer of cells that other genera colonize.

Compositional changes in the Guarinó River were observed during different hydrological periods associated with genera that had different adaptations or requirements. During the driest periods that occurred during El Niño, high water transparency, moderate water depth and water velocity, and prolonged sunlight periods would have favoured the development of Chlorophyta and Charophyta (Luque and Martínez de Fabricius, 2003), especially filamentous genera, such as *Cladophora, Chaetophora, Spirogyra* and *Mougeotia*, that form threads or manes that entwine and form dense mats because the environmental conditions stimulated their growth. These genera are selected by a vertical growth habit that allows greater access to light and nutrients from the water column (Margalef, 1983). They can even form more available and suitable substrates for diatoms, so they create a commensal relationship; they are considered to be an important structuring agent for the phycoperiphyton distribution. According to Andramunio-Acero (2013), filamentous genera are the most abundant and have a three-dimensional form; they frequently have a metaphytic habitat and improve habitat complexity. In contrast, *Chroococcus* and *Oscillatoria (Cyanobacterias)* develop an abundant mucilaginous matrix that allows the attachment of cells and improves stress tolerance during high flow periods (Becerra and Tavera, 2003). Diatoms that grow under high flow stress attach more strongly and have higher resistance to drifting; they are selected by attachment forms that act as ecological adaptations, such as prostrate, adnate, erect, peduncles, fimbriae, or tubes, or develop mucilaginous matrices (Siqueiros-Beltrones and Argumedo-Hernández, 2005). These forms of adherence allow many of the most common genera in the Guarinó River to remain attached to the

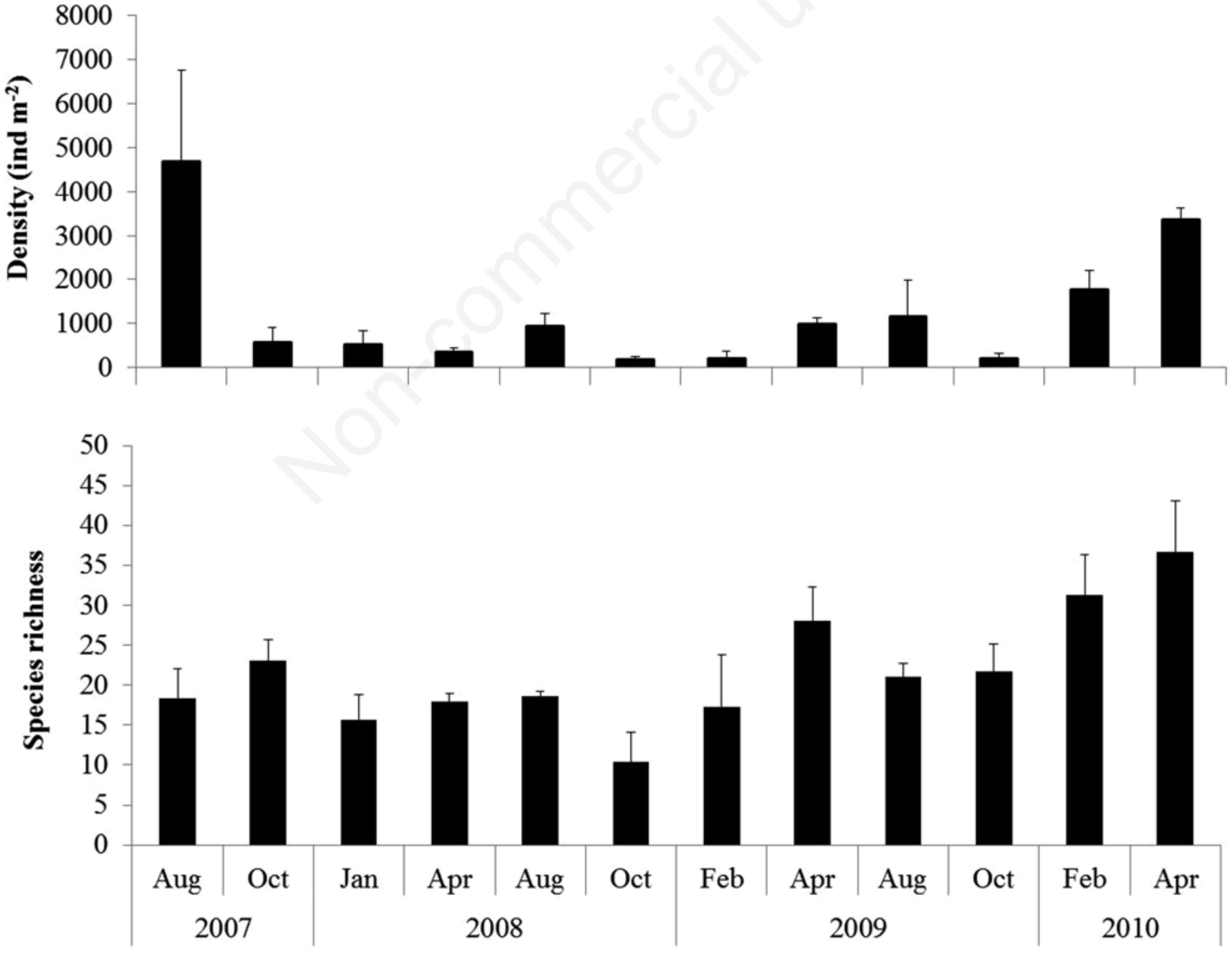

Fig. 6. Average values by hydrological period for the density and richness of phycoperiphyton genera of the Guarinó River between 2007 and 2010.

substrate surface. Such is the case for *Melosira*, a genera that is selected by stable environments, facilitating the establishment of large colonies or filaments, and is a typical slow colonizer under low speed of water (Pedraza-Garzón and Donato-Rondón, 2011).

As previously mentioned, Bacillariophyceae was the most representative class in the assemblage and has morphological characteristics that prevent its detachment and improve its resistance capability in flow fluctuations or during conditions of water movement that would cause scouring (Roldán and Ramírez, 2008). Such characteristics explain the frequency and abundance of Bacillariophyceae in lotic ecosystems where the hydrologic gradient is very pronounced. Particularly, *Fragilaria, Nitzschia, Gomphonema* and *Navicula* showed a wide environmental tolerance (Ramírez and Viña, 1998). *Fragilaria* form linear chains (Bicudo and Menezes, 2006) with an erect growth morphology, but spines or mucilage excretions allow for the joining of several valves (Rimet and Bouchez, 2012). *Fragilaria* is a genera of tall stature, the first gender form linear chains (Bicudo and Menezes, 2006) because spines or mucilage excretions allow for the joining of several valves (Rimet and Bouchez, 2012), while *Gomphonema* attached via mucilaginous stalks produced via apical pore fields (Sabater, 2009; Rimet and Bouchez, 2012), in addition to promote fixation, these stalks improve the relationship with the substrate, so *Gomphonema* can exploit resources that are unavailable to other genera. *Fragilaria* and *Gomphonema* were usually found in the upper sections of the mats (Tuchman and Stevenson, 1991). *Nitzschia* usually attaches to the substrate apically and perpendicularly with its valve. *Navicula* is a bidimensional gender because it produces a mucilage secretion that ties up the raphe and keeps the cells adhered to the substrate (Andramunio-Acero, 2013).

Genera that had significant densities during environmentally different seasons and years are adapted to changes in the environmental conditions of the river. An example is *Lyngbya,* one of the most representative genera in the assemblage. It was prevalent during both dry and high flow seasons because it has the capability of developing a mucilaginous matrix that, in addition to adhering the cells to the substrate during high flow seasons, prevents the dehydration of the reproductive organs when the water level decreases; therefore, when the humidity conditions are better, it is rapidly activated (Casco and Toja, 2003). Another example is *Melosira*, a colonial diatom that forms long chains of cells attached to the substrate via a mucilaginous strand that persisted during both low and high water periods (Andramunio-Acero, 2013) although it is typical in low periods. This result is contrasting those of Passy (2007) and Rimet and Bouchez (2012), who consider this genera as a disturbance stressed organism. We supposed that the presence of *Melosira* was defined primarily by other factors and not physical disturbances. It can be conclude there is still no consensus on a uniform treatment of growth forms with respect to it ecological responses. Our result also confirmed the pos-

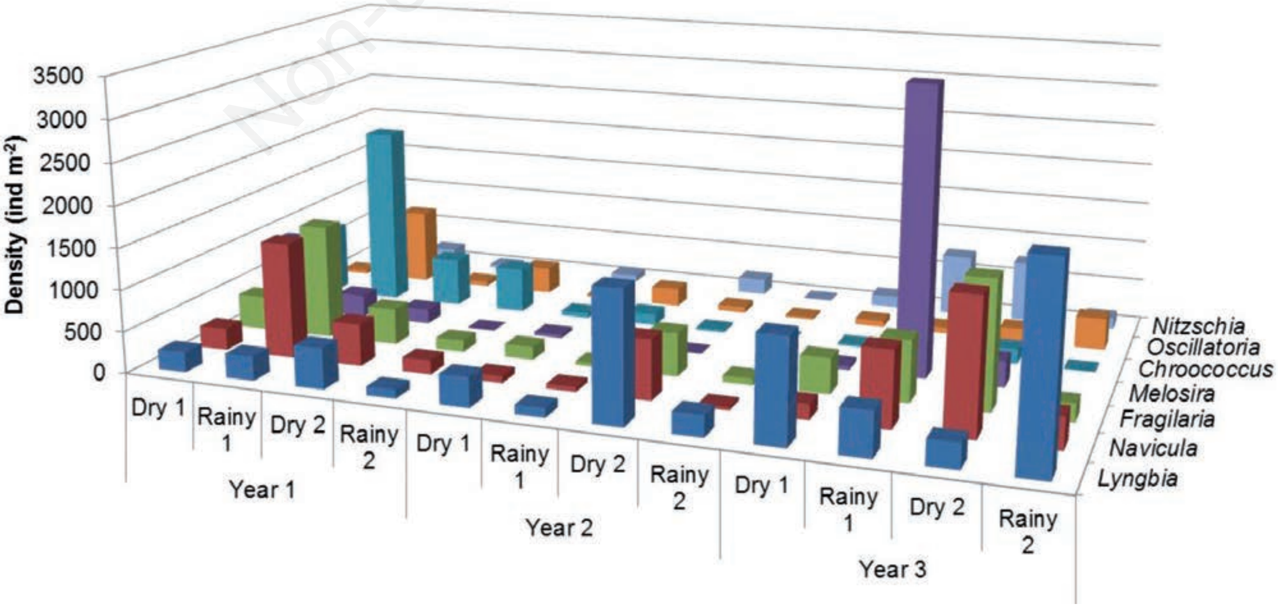

Fig. 7. Axis I of Discriminant Analysis applied on the density of the phycoperiphyton genera and environmental variables of the Guarinó River between 2007 and 2010.

sible necessity of revising the resistance of this genera to physical disturbance.

For benthic organisms, such as algae, exclusion or mortality could be high in environments with recurrent hydrological disturbances (Larned, 2010; Larson and Passy, 2012; Rickard *et al.*, 2004). However, many genera develop strategies and mechanisms to persist in the substrate after severe disturbances, maximizing their chance to remain attached and to recover from the disturbance (Biggs and Smith, 2002; Biggs *et al.*, 2005). The irregular distribution of the phycoperiphyton in systems that experience hydrological disturbances facilitates the proliferation of organisms of different groups. Moreover, the rapid immigration of some populations reduces the effect of a disturbance and allows rapid recolonization and succession of the assemblage, allowing for recovery from the disturbance in days or weeks (Biggs and Smith, 2002; Zapata and Donato, 2005; Felisberto and Rodrigues, 2010). It is important to consider that in the Guarinó River, the effectiveness of this process could be limited by the magnitude of the hydrological disturbance, and immigrants are precursors of the phycoperiphyton that grow because even strongly attached organisms, such as some diatoms, could be eliminated by a disturbance.

The values for the total algal density did not show high dependence on the flow, probably due to the predominance of specific growth forms that were adapted to flow fluctuation; however, changes in the diversity and composition were observed. Many studies report an inverse relationship between the flow and diatom diversity and density (Lamb and Lowe, 1987; Mosisch and Bunn, 1997; Ghosh and Gaur, 1998; Ryder *et al.*, 2006), and it has even been suggested that better assemblage development occurs in intermediate flow regions (Martinez and Donato, 2003; Diaz and Rivera, 2004; Stevenson, 1996).

A positive response of the algal richness during stabilization periods after Niña-Niño transitions (*i.e.*, a moderate hydrological disturbance) and a high variability in rare genera leads to the conclusion that phycoperiphyton in the Guarinó River responds to hydrological variability according to the disturbance model predictions. Under conditions that can be considered to be an *ecological disturbance*, phycoperiphyton richness increased because the temporary action of the flow could create new ecological niches and improve the river dynamics, in addition to facilitating the dispersion of taxa that are mainly characterized by loosely attached forms (Pedraza-Garzón and Donato-Rondón, 2011; Passy, 2007; Algarte *et al.*, 2014). However, during long-term flooding periods of high magnitude, which are present during La Niña, richness and density decrease because the disturbance promotes the dragging or drifting of the organisms or affects the resources that they require.

Biggs and Smith (2002) concluded that long-term pe-

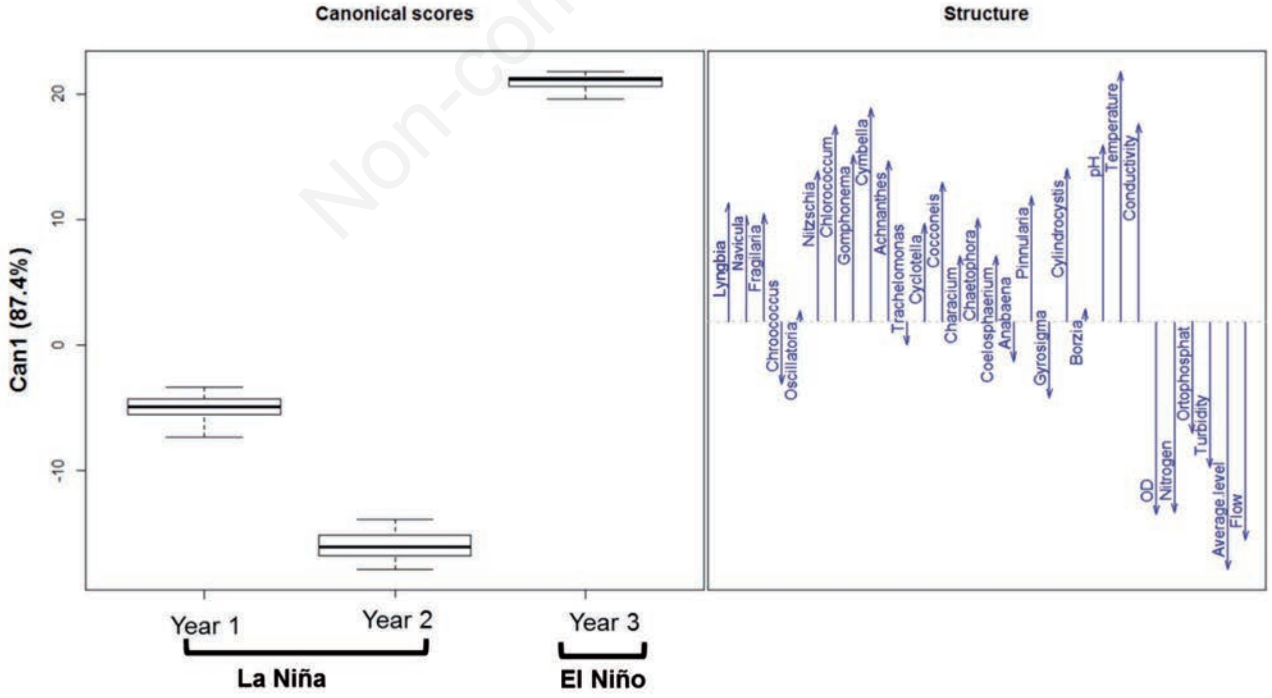

Fig. 8. Total density for the most abundant phycoperiphytic genera collected in Guarinó River during hydrological periods between 2007 and 2010.

riods of hydrological stability are necessary for the development of a highly rich phycoperiphyton assemblage in a specific stream. The prevalence of interannual differences of seasonality confirmed the homogenization effect on the assemblage during extreme rainfall and drought, forming different stable conditions during each year. However, in spite of the disturbances between wet and dry years, richness remained relatively high, and less seasonal variations in this variable were observed because the hydrological changes could have caused the replacement of genera governed by adaptations to particular environmental conditions. Such is the case for *Anabaena, Oscillatoria, Trachelomonas,* and *Chroococcus*, which were predominant during rainy periods; *Nitzschia, Synedra, Oedogonium, Cymbella, Gomphonema, Cocconeis, Achnanthes* and *Pinnularia*, which were predominant during drier periods; or the abundance of diatoms and green algae during El Niño, which were organisms that could withstand a moderate water velocity and prolonged periods of light.

A direct relationship between the algal assemblages and parameters, such as pH and temperature, was observed. The pH is involved in the phycoperiphyton metabolism because algae grow better in a basic or mildly alkaline media; under such conditions, nutrients such as carbonates and bicarbonates are more available (Roldán and Ramirez, 2008). Although temperature is not decisive for tropical phycoperiphyton, some groups, such as cyanobacteria (*Anabaena, Chroococus, Oscillatoria, Microcystis*) and Chlorophytas (*Characium, Chaetophora and Oedogonium*), tend to have higher densities at high temperature because low temperature tends to reduce the metabolic rate (Roldán and Ramirez, 2008).

Although nutrient levels are considered to be important for algal primary production processes (Mulholland *et al*., 1991; Lange *et al*., 2011; Larson and Passy, 2012), they had relatively little influence on the phycoperiphyton richness and density in the Guarinó River. This is probably because the phycoperiphyton has a very low response to increases in nitrogen and phosphorus in the surrounding water column (Stevenson *et al*., 1996; Martinez and Donato, 2003) regarding the nutrient levels in the substrate. According to Horner *et al*. (1990), a direct relationship exists between water speed and nutrient availability for algae; an increase in the water velocity can cause a reduction of the thickness of the nutrient poor laminar sublayer, which can cause an increase in the velocity gradient in the boundary layer, increasing its slope, with a concomitant increase in the molecular diffusion rate around the algal cells. Increases in current velocity and turbulence can accelerate the algal metabolic rate promoting nutrient uptake and the removal of metabolic waste (Peterson, 1987). This suggests that the hydrological cycle also has an indirect effect over the phycoperiphyton assemblage through nutrient uptake, but it could only be evaluated with analysis nutrient substrate.

CONCLUSIONS

Although information about the impact of climatic variables on phycoperiphyton is limited, Hutchinson (1967) has previously demonstrated the potential influence of climate on the phytoplankton composition. Studies on phytoplankton communities in lakes and estuary have also shown a response to the El Niño phenomenon; for example, diatoms were most abundant in wet and normal water years, whereas flagellate groups were most abundant in dry and critically dry years (Lehman, 2000). The results of this study confirm that such environmental control also extends to the phycoperiphyton assemblage and is reflected by the nonlinear effects of climate change associated with El Niño on the phycoperiphyton assemblage in the Guarinó River. Changes in the assemblage density and composition were due to adaptive responses to the local disturbance regime, as predicted by the *Habitat Templet Theory* (Townsend and Hildrew, 1994), giving the phycoperiphyton high resilience or resilience to stochastic events, such as climatic changes.

Given the importance of the *bottom-up* control exerted by the phycoperiphyton on the community structure of the river and their dependence on hydrological variables, knowledge of their responses to natural hydrological alterations (ENSO) is important to ecosystem conservation. This information provides a reference for anthropogenic disturbances, such as flow regulation or stabilization, that are associated with the exploitation of water resources. Additionally, the results of this study show that the management models for Andean foothill rivers should consider the potential synergy between the anthropogenic flow regulation and hydrological changes caused by the ENSO phenomenon, which is becoming increasingly common due to climate change.

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