



Diversity and structure of periphyton and metaphyton diatom communities in a tropical wetland in Mexico

Diversidad y estructura de las comunidades de diatomeas del perifiton y el metafiton en un humedal tropical en México

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Abstract. We investigated the structure and diversity of diatoms in communities of metaphyton and periphyton from the wetland of El Edén Ecological Reserve, Quintana Roo, Mexico. In spite of the close association and communication between these communities, our comparisons reveal that the 2 communities have distinct species assemblages, with the periphyton being more diverse overall. We fit abundance curves for periphyton and metaphyton, and argue that our results are consistent with communities where environmental conditions play a more important role than competition in structuring diatom species assemblages.

Key words: Bacillariophyceae, diatom assemblages, competition, random recruitment, karstic wetlands.

Resumen. Investigamos la estructura y la diversidad de las comunidades de diatomeas en el metafiton y el perifiton del humedal de la Reserva Ecológica El Edén, Quintana Roo, México. A pesar de la cercana asociación entre estas comunidades, nuestro análisis revela que tanto el perifiton como el metafiton consisten de distintas asociaciones de especies y el perifiton es el más diverso. Las distribuciones de las abundancias de las especies de diatomeas satisfacen curvas de distribución log-normal; esto significa que en las comunidades estudiadas, las condiciones ambientales juegan un papel más importante que la competencia para determinar su estructura.

Palabras clave: Bacillariophyceae, asociaciones de diatomeas, competencia, reclutamiento al azar, humedales kársticos.

Introduction

El Edén Ecological Reserve (EER), Quintana Roo, Mexico, consists of wetlands noteworthy for their ubiquitous algal growths, which can be divided into periphyton and metaphyton. Periphyton is found growing as crusts during the dry season, and adheres to virtually any substrate during the rainy season when the wetland is inundated. Metaphyton, which floats on the water surface, is only found during the wet season and permanently at the shores of cenotes (sinkholes).

The most conspicuous elements of both communities are filamentous cyanoprokaryotes (Novelo and Tavera, 2003); however, numerous species of diatoms can be found growing on and among these filaments. The majority of

the species found in these growths has been documented in tropical areas of low salinity and have been described as alkaliphiles associated with karstic environments or at least indifferent to calcareous substrates (Novelo et al., 2007). Diatom populations found growing in these communities closely follow changes in the hydroperiod as well as differences in substrate and vegetation type present in different parts of the wetland area (Novelo and Tavera, 2003). However, the close association of periphyton and metaphyton communities and the potential for mixture due to annual patterns of inundation create the potential for substantial overlap in species assemblages. In this study we investigate the structure and diversity of diatom species in both communities. We show that the 2 communities are in fact distinct in their diatom assemblages, and argue that these differences are likely due to the change from a sessile to a free-floating life style conditions associated

with colonization of the metaphyton.

Materials and methods

Study area. El Edén Ecological Reserve is located 25 km NNE of the town of Leona Vicario, in the municipality of Lázaro Cárdenas, Quintana Roo, Mexico (Fig. 1). The rock substrate consists of carbonate from the Cretaceous/Tertiary boundary (Urrutia-Fucugauchi et al., 1996; Campos-Enríquez et al., 2004; Keller et al., 2004). Soils, varying in depth from 0-1m, have a paucity of organic material. Bedrock is composed of carbonate fragments and melted materials of low permeability (Urrutia-Fucugauchi et al., 1996). The water table is very close to the surface, such that elevation and soil depth determine the variability in patterns of inundation in wetland zones during and after the rainy season.

The numerous underground systems of water in the Yucatán Peninsula flow towards the coast (Schultz, 2005). These currents, along with the carbonate composition of the zone, promote the formation of karstic depressions which cenotes, caverns, and superficial orifices form (Perry et al., 2003; Campos-Enríquez et al., 2004; Keller et al., 2004) all of which can be found throughout the EER.

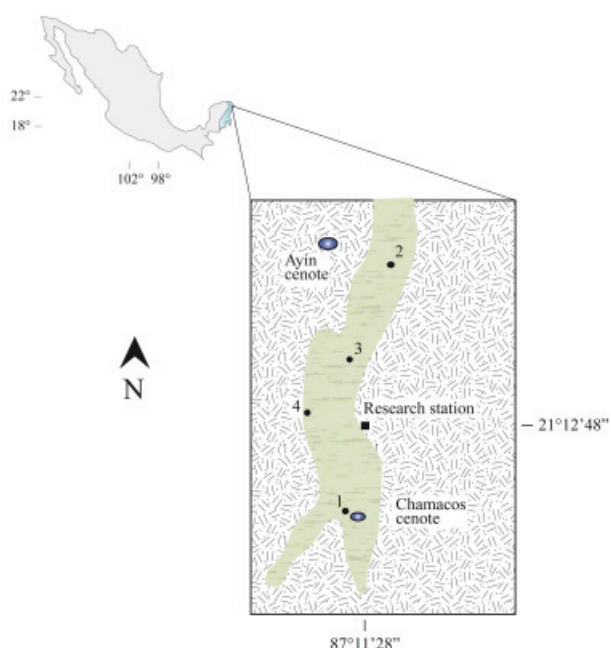


Figure 1. Location of El Edén Ecological Reserve and of the collection sites. 1-4 refer to the plots mentioned in the text. Ovals indicate position of cenotes and geographic coordinates locate the research station in EER. The inundated area inside EER is shaded in gray.

Sampling was carried out in July and October 1999 (the rainy season), April 2000 (the dry season), and August and November 2000 (also in the rainy season). Equal-volume random samples of periphyton and metaphyton were separately taken and fixed in 3% formaldehyde from cenotes and from each of 4 plots situated in the wetlands of the EER (described in detail in Novelo and Tavera, 2003). One cm² of metaphyton or periphyton was macerated by acid digestion (Rushforth et al., 1984) for extraction, cleaning and counting of diatoms. Permanent slides were mounted in Naphrax and observations of cleaned material were made with a Nikon E600 microscope, with differential interference contrast. Sampling sufficiency was tested by resampling individuals from the data to build accumulation curves (Gotelli and Colwell, 2001) for each community. Similarly, rarefaction curves and Shannon's index of diversity (Patrick, 1968; Krebs, 1999; Gotelli and Colwell, 2001) were used to compare species richness, equitability, and diversity in each of the 2 communities, since the overall sample size of diatom cells was different in each community. Both curves were calculated and graphed using the software package EcoSim (Gotelli and Entsminger, 2004). We calculated measures of equitability (E) and diversity (H) for each community and compared the assemblage of species using the inverse coefficient of Canberra's distance. Absent species were assigned a value of 0.1 following Krebs (1999) to avoid overvaluing species' presence and to equilibrate the data matrix. We used the R statistical software package Vegan 1.8-2 (Dixon, 2003) to fit rank-abundance data from each community to several abundance distributions as suggested in Wilson (1991).

Results

We identified 126 species of diatoms (Novelo et al., 2007) in 107 samples of periphyton and metaphyton from 4 plots in the wetland zone of the EER. Although 75% of the species are shared between the 2 communities (Table 1), an inverse coefficient of Canberra's distance of 0.16 suggests that they are nonetheless distinct. Both communities have unique species (9 in metaphyton and 31 in periphyton), and the frequency and relative abundance of individual species differ between communities as well. Both have a low frequency of rare species (12% in metaphyton vs. 16% in periphyton, Table 1). *Brachysira microcephala* (Grunow) Compère was the dominant species in the wet metaphyton and very abundant in wet periphyton. *Cymboplectra chacii* Novelo, Tavera et Ibarra, *Encyonema mesianum* (Cholnoky) D.G. Mann and *Mastogloia elliptica* (C. Agardh) Grunow were dominant in the wet periphyton.

Table 1. Presence of diatom species in metaphyton and periphyton in wet and dry seasons. Parentheses are used to highlight rare species. Abundant species are represented by the symbol Ø. DP=dry periphyton, DM=dry metaphyton, WP=wet periphyton, WM=wet metaphyton

<i>Species</i>	<i>DP</i>	<i>DM</i>	<i>WP</i>	<i>WM</i>
<i>Achnanthes inflata</i> (Kützinger) Grunow			*	(*)
<i>Achnanthidium chlidanos</i> (Hohn et Hellerman) Novelo, Tavera et Ibarra			*	*
<i>Achnanthidium exiguum</i> (Grunow) Czarnecki			*	(*)
<i>Achnanthidium minutissimum</i> (Kützinger) Czarnecki			*	*
<i>Achnanthidium minutissimum</i> var. <i>gracillima</i> (Meister) Lange-Bertalot		*	*	
<i>Amphipleura chiapasensis</i> Metzeltin et Lange-Bertalot				*
<i>Amphora coffeaeformis</i> (Agardh) Kützinger			*	*
<i>Amphora copulata</i> (Kützinger) Schoeman et Archibald			*	
<i>Amphora pediculus</i> (Kützinger) Grunow			*	
<i>Amphora veneta</i> Kützinger			*	*
<i>Anomoeoneis sphaerosphora</i> (Ehrenberg) Pfitzer			*	*
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	(*)		*	*
<i>Brachysira microcephala</i> (Grunow) Compère	*	*	Ø	Ø
<i>Caloneis bacillum</i> (Grunow) Cleve			*	*
<i>Caloneis sabanicola</i> Novelo, Tavera et Ibarra			*	*
<i>Caloneis silicula</i> (Ehrenberg) Cleve			*	*
<i>Campylodiscus hibernicus</i> Ehrenberg			(*)	
<i>Capartogramma crucicula</i> (Grunow ex Cleve) R. Ross			*	*
<i>Capartogramma paradisiaca</i> Novelo, Tavera et Ibarra			(*)	
<i>Cocconeis placentula</i> Ehrenberg var. <i>placentula</i>			*	(*)
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenberg) Cleve			*	(*)
<i>Cocconeis placentula</i> var. <i>lineata</i> (Ehrenberg) Cleve			*	
<i>Cocconeis pseudothumensis</i> E. Reichardt		*	(*)	
<i>Craticula cuspidata</i> (Kützinger) D.G. Mann			*	*
<i>Cyclotella meneghiniana</i> Kützinger			(*)	*
<i>Cyclotella ocellata</i> Pantocsek			(*)	*
<i>Cymbella aspera</i> (Ehrenberg) Cleve			*	
<i>Cymbella cistula</i> (Hemprich et Ehrenberg) Kirchner			*	(*)
<i>Cymbella mexicana</i> (Ehrenberg) Cleve			*	*
<i>Cymboplectra chacii</i> Novelo, Tavera et Ibarra	*		Ø	*
<i>Cymboplectra hustedtii</i> (Krasske) com. nov.	(*)			*
<i>Denticula kuetzingii</i> Grunow	*		*	*
<i>Denticula valida</i> (Pedicino) Grunow			*	
<i>Diademsia confervacea</i> Kützinger			*	
<i>Diatoma mesodon</i> Kützinger			(*)	
<i>Diploneis elliptica</i> (Kützinger) Cleve			*	*
<i>Diploneis oblongella</i> (Nägeli) Cleve-Euler			*	*
<i>Diploneis ovalis</i> (Hilse) Cleve			*	*
<i>Diploneis subovalis</i> Cleve				(*)
<i>Encyonema densistriata</i> Novelo, Tavera et Ibarra	(*)		*	*
<i>Encyonema mesianum</i> (Cholnoky) D.G. Mann	(*)		Ø	*
<i>Encyonema mexicanum</i> Krammer			Ø	*
<i>Encyonema neogracile</i> Krammer	(*)		*	*
<i>Encyonema silesiacum</i> (Bleisch) D.G. Mann			*	(*)
<i>Encyonopsis cesatii</i> (Rabenhorst) Krammer			*	(*)
<i>Encyonopsis microcephala</i> (Grunow) Krammer			*	*
<i>Encyonopsis ruttneri</i> (Hustedt) Krammer				(*)
<i>Eolimna subminuscule</i> (Manguin) Moser, Lange-Bertalot et Metzeltin	*	*	*	*
<i>Epithemia sorex</i> Kützinger			*	*
<i>Epithemia turgida</i> (Ehrenberg) Kützinger			*	
<i>Eunotia camelus</i> Ehrenberg var. <i>camelus</i>			*	*
<i>Eunotia camelus</i> var. <i>arcuata</i> Frenguelli			*	*
<i>Eunotia flexuosa</i> (Brébisson) Kützinger			*	*
<i>Eunotia formica</i> Ehrenberg			*	

<i>Species</i>	<i>DP</i>	<i>DM</i>	<i>WP</i>	<i>WM</i>
<i>Fragilaria capucina</i> var. <i>vaucheriae</i> (Kützing) Lange-Bertalot			*	*
<i>Frustulia vulgaris</i> (Thwaites) De Toni	(*)		*	
<i>Gomphonema acuminatum</i> Ehrenberg			*	*
<i>Gomphonema affine</i> Kützing			*	(*)
<i>Gomphonema gracile</i> Ehrenberg	(*)		*	*
<i>Gomphonema parvulum</i> Kützing			*	*
<i>Gomphonema truncatum</i> Ehrenberg			*	*
<i>Gomphonema vibrioides</i> E. Reichardt et Lange-Bertalot			Ø	*
<i>Gomphonema</i> sp.			(*)	
<i>Gyrosigma obscurum</i> (W. Smith) Griffith et Henfrey			(*)	
<i>Gyrosigma scalproides</i> (Rabenhorst) Cleve			(*)	
<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow			*	*
<i>Karayevia clevei</i> (Grunow) Round			*	*
<i>Kobayasiella</i> sp.	*	*	*	*
<i>Martyana martyi</i> (Héribaud) Round			*	*
<i>Mastogloia elliptica</i> (C. Agardh) Grunow	*	*	Ø	*
<i>Mastogloia smithii</i> Thwaites ex W. Smith	*	*	*	*
<i>Melosira varians</i> C. Agardh	*	*	*	*
<i>Navicula cryptotenella</i> Lange-Bertalot			*	*
<i>Navicula erifuga</i> Lange-Bertalot			*	*
<i>Navicula heimansii</i> van Dam et Kooyman			*	*
<i>Navicula podzorskii</i> Lange-Bertalot			*	*
<i>Navicula radiosa</i> Kützing	*	*	*	*
<i>Navicula rivulorum</i> Lange-Bertalot et Rumrich			*	*
<i>Navicula rostellata</i> Kützing			*	
<i>Neidium ampliatus</i> (Ehrenberg) Krammer			*	*
<i>Nitzschia amphibia</i> Grunow	*		*	*
<i>Nitzschia communis</i> Rabenhorst			*	
<i>Nitzschia frustulum</i> (Kützing) Grunow			*	*
<i>Nitzschia gracilis</i> Hantzsch			(*)	*
<i>Nitzschia inconspicua</i> Grunow				(*)
<i>Nitzschia intermedia</i> Hantzsch			*	*
<i>Nitzschia lacunarum</i> Hustedt				*
<i>Nitzschia linearis</i> W. Smith	*		*	(*)
<i>Nitzschia nana</i> Grunow			*	*
<i>Nitzschia palea</i> (Kützing) W. Smith			*	*
<i>Nitzschia palustris</i> Hustedt			*	*
<i>Nitzschia vitrea</i> Norman			*	
<i>Pinnularia borealis</i> Ehrenberg				(*)
<i>Pinnularia certa</i> Krammer et Metzeltin			*	*
<i>Pinnularia divergens</i> W. Smith			*	
<i>Pinnularia gibba</i> (Ehrenberg) Ehrenberg			*	*
<i>Pinnularia major</i> (Kützing) Rabenhorst			*	(*)
<i>Pinnularia mayarum</i> Novelo, Tavera et Ibarra			*	
<i>Pinnularia microstauron</i> (Ehrenberg) Cleve	*		*	*
<i>Pinnularia streptoraphe</i> var. <i>parva</i> Krammer	(*)		*	*
<i>Pinnularia subgibba</i> var. <i>capitata</i> Metzeltin et Lange-Bertalot			*	*
<i>Pinnularia subrostrata</i> Lohman et Andrews			*	
<i>Placoneis porifera</i> var. <i>opportuna</i> (Hustedt) Novelo, Tavera et Ibarra.				*
<i>Planothidium lanceolatum</i> (Brébisson) Round et Bukhtiyarova			*	*
<i>Pseudostaurosira brevistriata</i> (Grunow) D.M. Williams et Round			(*)	*
<i>Rhoicosphenia abbreviata</i> (C. Agardh) Lange-Bertalot			*	*
<i>Rhopalodia gibba</i> (Ehrenberg) O. Müller			*	
<i>Rhopalodia musculus</i> (Kützing) O. Müller			*	
<i>Sellaphora guyanensis</i> Metzeltin et Lange-Bertalot			*	
<i>Sellaphora laevis</i> (Kützing) D.G. Mann	*	*	*	*
<i>Sellaphora pupula</i> (Kützing) Mereschkowsky			*	*

<i>Species</i>	<i>DP</i>	<i>DM</i>	<i>WP</i>	<i>WM</i>
<i>Sellaphora stroemii</i> (Hustedt) D.G. Mann	*	*	*	*
<i>Stauroneis amphibia</i> Novelo, Tavera et Ibarra	*	*	*	
<i>Stauroneis phoenicenteron</i> (Nitzsch) Ehrenberg			*	*
<i>Staurosira construens</i> Ehrenberg var. <i>construens</i>		*	*	
<i>Staurosira construens</i> var. <i>binodis</i> (Ehrenberg) P.B. Hamilton			(*)	(*)
<i>Staurosira construens</i> var. <i>venter</i> (Ehrenberg) P.B. Hamilton			*	
<i>Staurosirella pinnata</i> (Ehrenberg) D.M. Williams et Round				*
<i>Stephanodiscus hantzschii</i> Grunow			*	*
<i>Surirella biseriata</i> Brébisson			*	
<i>Surirella brebissonii</i> Krammer et Lange-Bertalot			*	
<i>Surirella tenera</i> W. Gregory	*	*	*	
<i>Thalassiosira visurgis</i> Hustedt	*	*	*	*
<i>Tryblionella hungarica</i> (Grunow) Frenguelli				(*)
<i>Ulnaria acus</i> (Kützinger) Aboal			*	*
<i>Ulnaria ulna</i> (Nitzsch) Compère	*	*	*	*

Accumulation curves suggest that sampling in each community was sufficient: both curves leveled off to the asymptote at less than 80% of the observed species (Fig. 2).

Using the rarefaction curves, we can compare equal-sized samples from both communities and show that the periphyton has higher species richness (Fig. 3). Shannon's index of diversity suggests that the periphyton is also slightly more diverse ($H=3.55$) compared to metaphyton ($H=3.41$).

Rank abundance curves of diatoms in both communities better fit a log-normal distribution than any of the other distributions tested (broken stick, pre-emption, Zipf and Zipf-Mandelbrot models), using the Akaike information criterion (Fig. 4). This is reflected in the high equitability ($E>0.75$) of both communities. Neither highly abundant nor singleton species are particularly frequent, and the distribution is dominated by groups of species of intermediate abundance (between 14 and 80%, Fig. 4). This is consistent with a random recruitment of species in both communities.

Discussion

The majority of the diatoms in the EER can potentially grow in either periphyton or metaphyton. In fact, many species observed in the EER have been previously reported in both communities in other areas (Patrick and Reimer, 1966, 1975; Foged, 1984; Krammer, 1997a, 1997b; Krammer and Lange-Bertalot, 1985, 1986, 1988, 1991a, 1991b). During the brief periods of inundation, the development of diatom populations in both communities is expansive and rapid, with diatoms flourishing even in shallow waters. The difference in the composition of the diatom assemblages was evident from the list of species

observed (Table 1), and substantiated by calculation of Canberra's distance.

The development of diatom populations in the metaphyton depends on the presence of a water column, present only during the rainy season in most parts of the EER. Sample size is therefore lower for the metaphyton, making a comparison of richness difficult; rarefaction curves circumvent this problem and confirm the higher species richness of the periphyton.

Rank abundance distributions of diatoms from both periphyton and metaphyton fit well to a log-normal model, which describes communities in development, where interspecific competition is less important in causing species rareness. In the EER, diatom community structure is undoubtedly affected by changes in the hydroperiod. Not only does inundation dislodge diatoms in the periphyton, thus contributing to the formation of the metaphyton and a change from a sessile to a free-floating life style, but also brings about changes in light, temperature, and nutrient availability (Novelo and Tavera, 2003). The response of diatom populations in the metaphyton to these varied changes must be rapid: in spite of environmental change in a short period of time, diatoms in the metaphyton are nearly as diverse and equitable as their counterparts in the periphyton.

Therefore, in the EER, it is likely not interspecific competition but the ecophysiological response to a changing environment that determines species distributions. Caswel (1976) shows that biological interactions such as interspecific competition generally reduce diversity within communities. This is not seen in communities in the EER, even when considering the effect of inundation. This interpretation also finds support in May (1975), who argues that under a lognormal distribution model, species are generally independent and sufficiently numerous to

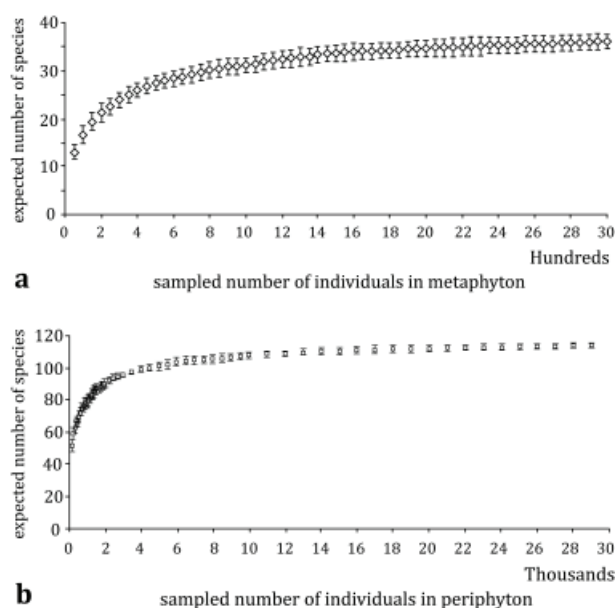


Figure 2. Accumulation curves for metaphyton (a) and periphyton (b).

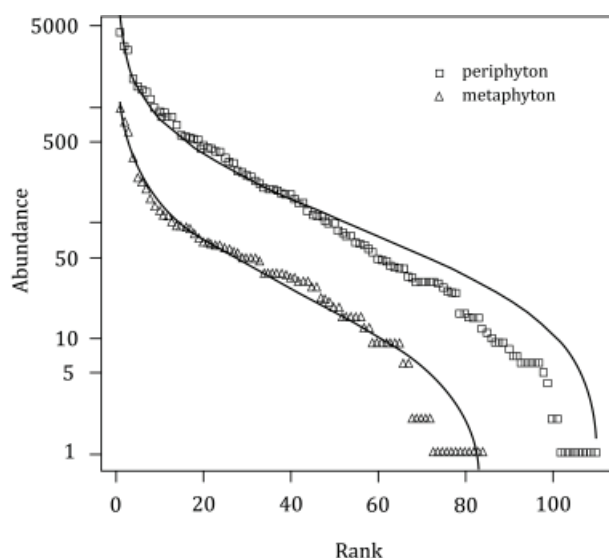


Figure 4. Rank-abundance curves for metaphyton and periphyton communities. Solid lines show the expected best-fit curve. $\log \mu$ periphyton = 4.50, metaphyton = 3.18; $\log s$ - periphyton = 1.61, metaphyton = 1.53; deviance periphyton = 1610.66, metaphyton = 217.50.

survive small migrations.

Characterization of the taxonomy and environmental affinities of the diatoms of the EER (Novelo et al., 2007) has shown that species composition of diatom

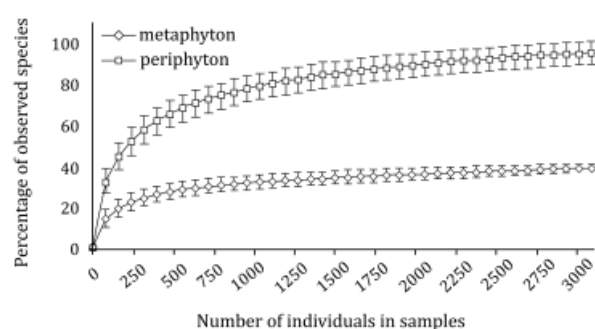


Figure 3. Rarefaction curves for metaphyton and periphyton. Percentage of species observed in each community.

communities in the EER varies across latitude and the physiological capacities of the species change in relation to the environmental factors of the wetland. The present study analyzes the structure of diatom communities in the periphyton and metaphyton, and uses this analysis to describe the changes in the species composition of these communities as a result of the hydrological cycle. We still know little about the ecology of freshwater algae, and this work is among the first to treat the community structure of tropical diatoms in general terms. We suggest that models of algal community ecology in karstic seasonal wetlands need to take into account the movement and colonization of diatom species.

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