# Decoupled lake history and regional moisture availability in the middle elevations of tropical Mexico

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## ABSTRACT

During the Holocene, most of the climatic variability in the tropics has manifested through changes in the precipitation regime. Although there is relatively a large amount of information on this climatic variability from the lowlands during this time period, little is known regarding the environmental variability in the middle elevations. Here we present evidence of environmental change from a lacustrine sedimentary record recovered from Lake Lacandón, a small shallow water body located in the middle elevations of Chiapas, Mexico. Through analyses of cladoceran assemblages and chemical properties of the sediments (concentrations of C, Ca, N, Rb, Sr, Ti, and Zr), we aimed to reconstruct local and regional environmental conditions during the last 4,000 years. Our results show a highly dynamic cladoceran community apparently associated with changes in the size of the lake, which although variable has been enlarging through the last 4,000 years. Geochemical evidence also suggests high variability in moisture availability overimposed on a general trend towards drier conditions. Whereas the growing lake size seems associated with decreasing insolation seasonality, the trend to drier regional climates corresponds to the well-known southward displacement of the Intertropical Convergence Zone through the Holocene. Although the regional climate has been deteriorating, the enlarging lake suggests a decreasing water deficit though time. This pattern is probably a result of increasing insolation during the dry season, causing advection of marine moisture that precipitates because of the steep elevation gradient. Our results highlight the intricate nature of the millennial scale environmental variability, and the potential role of the middle elevations for sheltering biodiversity through times of environmental hardship.

Key words: tropical Mexico; paleoecology; paleoclimatology; cladocerans; geochemistry.

## RESUMEN

*Durante el Holoceno la mayor parte de la variabilidad climática en los trópicos se manifestó a través de cambios en los regímenes de precipitación. En este sentido, existe una cantidad de información relativamente extensa con respecto a la variabilidad climática en las tierras bajas, mientras poco se conoce en relación a la variabilidad ambiental de las elevaciones medias. En este trabajo presentamos evidencia de cambios ambientales derivada de una secuencia sedimentaria recuperada en el Lago Lacandón, un cuerpo de agua somero y pequeño ubicado en las elevaciones medias del Estado de Chiapas, México. Mediante el análisis de algunas propiedades químicas de los sedimentos (concentraciones de C, Ca, N, Rb, Sr, Ti, y Zr) y los ensambles de cladóceros contenidos por los mismos, abordamos la reconstrucción de las condiciones ambientales locales y regionales a través de los últimos 4,000 años. Los resultados mostraron una comunidad de cladóceros altamente dinámica en el tiempo que ha estado aparentemente asociada con el tamaño del lago. Los cladóceros muestran que, aunque variable, el tamaño del cuerpo de agua ha mostrado una tendencia creciente a través del tiempo. La evidencia geoquímica también muestra alta variabilidad en la disponibilidad de humedad*

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*regional superpuesta sobre una tendencia general hacia condiciones más secas. Mientras el crecimiento del tamaño del lago podría estar asociado a una reducción en la estacionalidad de la insolación, la tendencia hacia condiciones más secas parece asociada a la bien conocida migración hacia el sur de la Zona Intertropical de Convergencia a través del Holoceno. Aunque el clima regional se ha ido deteriorando, el crecimiento del lago sugiere una reducción en el déficit anual de humedad. Este patrón es probablemente el resultado del aumento en la insolación d urante las estación seca, el cual causaría advección de aire húmedo desde el mar, el cual precipitaría dado el gradiente orográfico. Los resultados de este estudio demuestran la naturaleza compleja de la variabilidad ambiental a escala de milenios, y el papel potencial de las elevaciones medias como refugios de diversidad durante tiempos de climas desfavorables.*

*Palabras clave: México tropical; paleoecología; paleoclimatología; cladóceros; geoquímica.*

## INTRODUCTION

Tropical climates through the Quaternary have been the result of a complex network of interactions among local, regional, and global drivers acting at different temporal and spatial scales (Bradley, 2015). During the Holocene (the last ~11,000 years), although conditions have been warmer on average, precipitation has represented an element introducing large amounts of variability into the tropical climate systems (*e.g.,* Hodell *et al.,* 1991; Haug *et al.,* 2001; Tedesco and Thunell, 2003; Bernal *et al.,* 2011). In the Yucatan Peninsula, precipitation variability through the Holocene has been largely documented based on sedimentary evidence (Hodell *et al.,* 2001; Anselmetti *et al.,* 2007; Mueller *et al.,* 2009; Wahl *et al.,* 2014). Apparently, the regional history has been characterized by alternating periods of wetness and drought that were variable in length, and a high influence of human populations on the landscape (Leyden, 2002).

Despite the relatively large amount of paleoenvironmental information that is available on the Holocene in the Yucatan Peninsula, little is known on the environmental history of the middle elevations (premontane and lower montane altitudinal belts of Holdridge *et al.,* 1964). Mid altitude environments might have been of vital importance for the survival of natural population during times of extreme environmental hardship (*e.g.*, Heinrich events during the Pleistocene, Correa-Metrio *et al.,* 2012). High topographic diversity and steep environmental gradients over relatively short distances make middle elevations regions with high potential for harboring microrefugia (Bush, 2002; Rull, 2009; Correa-Metrio *et al.,* 2014b). The orographic gradient offers conditions where rainfall is more likely, and therefore, the climatic trends of these regions are not necessarily coupled with those of the low flat terrains. However, there is still need to evaluate the role that these regions have played in terms of biodiversity preservation through time based on hard evidence. A first step towards this evaluation would be the understanding of local environmental trajectories in the context of regional climatic variability.

Much of the information gap derives from the fact that lakes in middle elevation are rather scarce. The Lacandón Forest region, southeastern tropical Mexico, is characterized by a series of karst water bodies located in middle elevations, providing a good setting for studying the evolution of local and regional environments through time. In this study, we aimed to infer environmental changes during the late Holocene (the last ~4,000 years). Geochemical indicators are useful to infer past conditions of sediment deposition (Last and Smol, 2001). We used, C, Ca, N, Rb, Sr, Ti, and Zr to infer erosion intensity and organic matter provenance, characteristics that provide information on past precipitation regimes and lake trophic status. Cladocerans are microcrustaceans whose chitinous shells are identifiable at species level and preserve well in lake sediments (Alonso, 1996; Smol *et al.,* 2003). Given their environmental specificity (Table 1), cladocerans are

Table 1. Environmental preferences of the principal cladoceran species from Lake Lacandón (environmental affinities from Bērziņš and Bertilsson, 1989; Alonso, 1996; Lotter *et al.,* 1998).

| **Species** | **Reported environmental preferences** |
|---|---|
| *Acroperus harpae* | Abundant in oligo- to meso-trophic water bodies. The species prefers littoral environments with clear waters and abundant aquatic vegetation. |
| *Alonella exigua* | Abundant in karstic environments with calcium-rich and weakly-mineralized waters. The species prefers littoral environments dominated by subaquatic plants with floating leaves. |
| *Alonella exisa* | Abundant in water bodies located between 500 and 1,500 meters of elevation above sea level with rather acidic waters. The species prefers mineralized transparent waters in littoral environments with submerged vegetation. |
| *Alona intermedia* | Abundant in oligotrophic water bodies with pH lower than 6.0. The species prefers weakly mineralized waters and sandy substrates. |
| *Alona ossiani* | Abundant in oligo- to meso-trophic water bodies. The species prefers littoral environments with abundant vegetation in clear weakly-mineralized waters. |
| *Alonella nana* | Abundant in littoral environments with abundant vegetation. The species is found in weakly-mineralized peaty waters and also in karstik environments. |
| *Bosmina coregoni* | Planktonic species commonly found in eutrophic environments. The species has also been often associated with abundant fish population in the water body. |
| *Bosmina longirostris* | Planktonic species associated with alkaline waters. The species has been usually associated with high phosphorous concentrations in the water. |
| *Bosmina longispina* | Planktonic species commonly associated with acidic environments. The ecological succession from this species to *Bosmina coregoni* is a clear indicator of eutrophication processes. |
| *Chydorus* cf. *sphaericus* | Although the species has been reported as ecologically generalist, its dominance is usually an indicator of eutrophication. It is usually found living in the substrate. |
| *Coronatella rectangula* | Littoral species commonly associated with high calcium concentrations. |
| *Eurycercus lamellatus* | Abundant in littoral environments with clear waters and abundant vegetation. |
| *Leudigia louisi* | Littoral species abundant in weakly mineralized waters. The species is adapted to living in the mud and is apparently favored by the presence of abundant vegetation. |

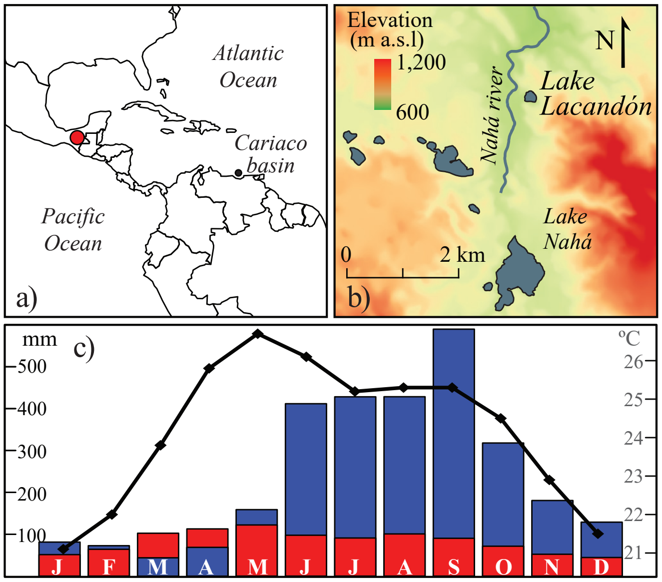


Figure 1. Study area. a) The localization of the Lacandón Forest in southeastern Mexico. b) Details on the topographic context of Lake Lacandón. c) Climograph from Lacatún meteorological station; monthly precipitation (blue bars) and potential evapotranspiration (red), and monthly mean temperature (black line); data from Servicio Meteorológico Nacional (2016).

good indicators for reconstructing limnological conditions (Smol *et al.,* 2003). We use changes in the cladoceran assemblages for infering water depth and lake trophic status. Our main questions are: i) What has been the general trend of precipitation in the Lacandón Forest through the last 4,000 years?, ii) Apart from the general trend, has there been a systematic higher frequency mode of variability? and iii) has the climatic variability in the middle elevations been linked to the variability reported for the lowlands?.

## METHODS

### Study area

Lake Lacandón is located in the State of Chiapas, Mexico (17°00'55.80"N, 91°35'23.34"W, 810 m a.s.l.) near the protected area of Nahá, northwest region of the Lacandón Forest (Figure 1). With an area of ~1 ha and a maximum depth of ~3 m in its central part, the lake lies on a karstic platform of marine Cretaceous origin, with inclusions of continental lutites and sandstones (Padilla y Sánchez, 2007). Mean annual precipitation in the region is ~1,860 mm, with 92% of it concentrated between May and December (climate data from Lacantún meteorological station, Servicio Meteorológico Nacional, 2016). Mean annual temperature is 23.6 °C, with the coldest and warmest temperatures at 20.9 and 25.6 °C during January and May, respectively. The regional vegetation is a mosaic composed of tropical rain forest, cloud forest, coniferous forest, secondary vegetation and large agricultural areas and pastures (Rzedowski, 2006).

### Data collection and analyses

In July 2012 a 370 cm long sedimentary sequence, core LAC12-I, was recovered from Lake Lacandón using a modified Livingstone piston corer (Colinvaux *et al.,* 1999). Given the consistency of the sediment, the core was bagged in the field and samples were split into a half that was stored as archive, and the other was used for the paleoenvironmental analyses. The lithology was described qualitatively (color, texture and reaction to HCl). Chronological control of the sequence was derived from two pollen extracts submitted to AMS (accelerator mass spectrometry) radiocarbon dating. The samples were extracted from the bottom of the core (369 cm below lake floor, blf hereafter) and from its middle part (118 cm blf), and the analysis was carried out at Beta Analytic Inc. (Miami, Florida). Radiocarbon dates were calibrated and a Bayesian depth-age model was built using Bacon (Blaauw and Christen, 2011). All dates were expressed as calendar years before present (BP hereafter).

The core was sub-sampled every 5 cm for cladoceran and geochemical analysed. For cladoceran counts, 1 cc samples were defloculated using KOH, and carbonates were dissolved with HCl. Samples were then analyzed under a microscope at magnifications 100X and 400X, aiming at a count of 200 individuals containing all the remains found (headshields, shells, postabdomens, postabdominal claws, and ephippia). Cladocera were identified to species level using illustrated guides (Elías-Gutiérrez *et al.,* 1997; Szeroczyńska and Sarmaja-Korjonen, 2007; Elias-Gutierrez *et al.,* 2008). Cladoceran counts were expressed in terms of relative abundance and plotted stratigraphically using the software *C2 Data Analysis* (Juggins, 2007). For geochemical analyses, 1 cc samples were oven-dried at 40 °C, homogenized and ground with an agate mortar. Concentrations of Ca, Rb, Sr, Ti and Zr were measured with a portable Thermo Scientific NITON FXL 950 X-Ray Fluorescence (XRF) analyzer. Total carbon and nitrogen were measured by duplicate using lyophilized sediment from the same depths through an elemental analyzer CNHS/O Perkin Elmer 2400 series, and the ratio C:N was calculated.

Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980) was performed on the biological data using all species found to summarize environmental changes along the record (Correa-Metrio *et al.,* 2014a). The association among geochemical variables was estimated through Pearson correlation coefficients (Legendre and Legendre, 1998), whose *p*-values were corrected for family wise error (Zar, 1999). All statistical analyses were conducted using the statistical software environment R (R Core Team 2015), particularly package vegan (Oksanen *et al.,* 2015).

## RESULTS

From the bottom of the record (370 cm blf) to 270 cm blf, the sediment consists of silty clays with interbedded bands of sand or organic mud (Figure 2). From 270 to 200 cm blf, the sediments were composed of coarser materials, mainly a 20 cm wide sand layer (from 270 to 250 cm blf) and silts from 250 to 200 cm blf. From 200 cm blf to the top of the record, sediments were mainly composed of clays with two layers of organic mud, one from ~200 to 162 cm blf, and the other representing the upper ~15 cm of the record. According to the calibrated age model (Table 2 and Figure 2), the sedimentary record spans the last ~4,000 years, *i.e.* the late Holocene (Walker *et al.,* 2012), with high (low) sedimentation rates in the lower (upper) half of the core.

Approximately 70,000 individual cladocerans were found in the 77 analyzed samples. The record was composed of 16 species: three planktonic or open water species (family Bosminidae) and 13 littoral species (family Chydoridae) (Figure 3 and 4). The family Chydoridae was present through the entire record, except for the interval between 261 and 194 cm blf (~3,100 and 2,550 BP) where samples were barren of cladocerans. The family Bosminidae was abundant from 170 cm blf (~2,350 BP) to the top of the core (present).

The lengths of DCA, Axes 1 and 2 in the ordination of species (samples) were 4.94 (3.16) and 3.94 (2.26) standard deviations (SD), respectively (Figure 5). The highest scores of Axis 1 corresponded

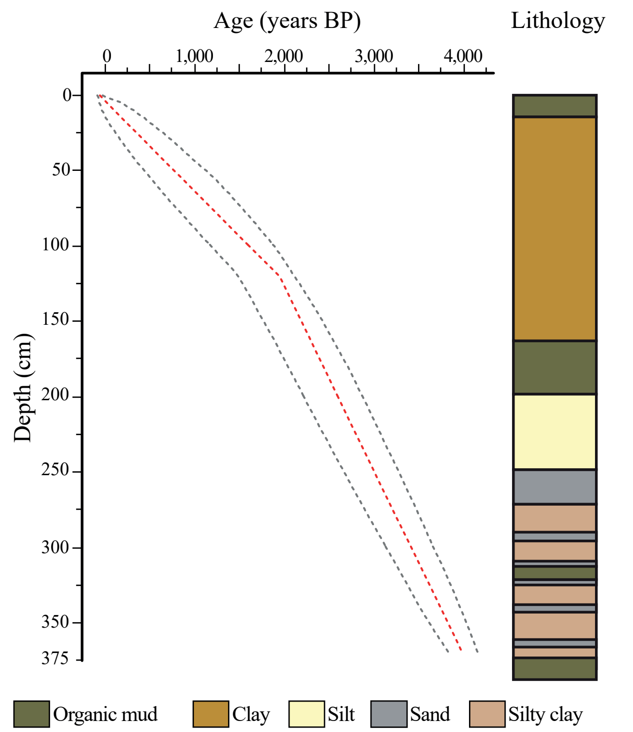


Figure 2. Chronological model. Age in years before present (BP) as a function of depth in cm below lake floor. The lithological description is included on the right.

to *Leydigia louisi*, followed by *Camptocercus dadayi* and *Coronatella rectangula*, whereas the lowest scores corresponded to *Bosmina longirotris*, *Eurycercus* sp. and *Bosmina* (*E.*) *longispina* (Figure 5). The highest scores of DCA Axis 2 corresponded to *Acropercus harpae*, *Graptoleberis testudinaria* and *Alonella exigua*, whereas the lowest scores were assigned to *Leydigia louisi*, *Coronatella rectangula* and *Alonella nana* (Figure 5). Samples older than 2,500 BP were ordinated in quadrants one and four, whereas those younger than 2,500 BP clustered in quadrants two and three (Figure 5).

Concentrations of the analyzed elements were highly variable through the record (Figure 3). C and N showed high variability but a general increasing trend towards present. Ca, Sr and C:N ratio showed variable high values from the bottom of the record up to ~180 cm blf, and a less variable lightly decreasing trend from ~180 cm blf to the top of the record. Positive highly significant correlations were determined between C and N, C:N and Ca, Ti and Rb, Rb and Zr, and Ti and Zr (Table 3). Negative highly significant correlations were determined between N and C:N, N and Ca, Ca and Rb, Ca and Ti, Ca and Zr, and Sr and Ti (Table 3).

## DISCUSSION

### The environmental signal of cladocerans and geochemistry in the sediments of Lake Lacandón

The most evident feature inferred from the cladoceran assemblages of Lake Lacandón was a clear distinction between species associated with littoral and open water areas of the lake. Our *a priori* distinction of these two groups (Table 1 and Figure 3; environmental affinities from Bērzinš and Bertilsson, 1989; Alonso, 1996; Lotter *et al.,* 1998) was confirmed by the ordination of species along DCA Axis 1 (Figure 5). DCA Axis 1 captures the principal underlying environmental factor that drives ecological changes through time (Correa-Metrio *et al.,* 2014a), which in Lake Lacandón seems lake size and depth. Species reportedly associated with littoral areas were mostly ordinated on the positive side of Axis 1, and planktonic species associated with deeper waters (namely *Bosmina* spp.) obtained negative scores. Thus, according to our interpretation of the cladoceran community, at Lake Lacandón, the main environmental factor that controlled Cladocera through time was lake size. Lake lowstands cause the development of dense macrophyte mats that in turn favors the dominance of the species we classified as littoral. Conversely, as lake size increases, there is also a slight deepening of its central area that forces microphytes to retreat towards the shallower edges, favoring the dominance of *Bosmina* spp. Indeed, DCA Axis 1 scores showed a time pattern that was closely associated with total percentage of littoral species (Figure 6). Thus, we interpret DCA Axis 1 as representative of relative lake size/depth.

The relationships among geochemical indicators were consistent with a strong climatic influence over these proxies. Ti is an element that has been traditionally interpreted as an indicator of erosive activity (Haug *et al.,* 2001). In tropical environments such as the Lacandón Forest, where the main erosive factor is the runoff produced by rainfall, Ti sequences can be inferred as changes in total annual precipitation and/or seasonality. Such is the case of our Ti record, whose high positive correlation with Zr and Rb (Table 3), both of them conservative lithogenic elements (Boës *et al.,* 2011), offers further support to our interpretation. Also, the negative significant correlation of Ti with Ca and Sr, both indicative of authigenic mineral precipitation during period of low lake level (Eugster and Hardie, 1978), point to Ti as an indicator of terrigenic input into Lake Lacandón.

### Lake trophic status through the last 4,000 years

Cladoceran assemblages composition through time suggest mesotrophic conditions during most of the studied time period (Alonso, 1996; Lotter *et al.,* 1998). An exception to this pattern was the short period between ~1,800 and 1,600, when high abundances of *Bosmina longirostris* suggest eutrophic conditions (Bērzinš and Bertilsson, 1989, Figure 3). However, it is difficult to infer trophic changes because of the dominance of lake size on the cladoceran signal of our record. Nevertheless, geochemical indicators also suggest mesotrophic conditions in the lake through the last 4,000 years. Theoretically, organic carbon to nitrogen ratios above 20 and below 10 are indicative of allochthonous and autochthonous carbon input, respectively (Meyers, 1997). The calculated C:N ratios for Lake Lacandón never dropped below 10 (absolute minimum 12.1 through the entire record, Figure 6), supporting our interpretation of mesotrophic conditions through the record. However, these ratios were based on total carbon, implying that our report represents the scenario of the maximum organic carbon to nitrogen possible values (*i.e.*, assuming all the carbon had an organic origin). From the bottom of the record to ~2,000 BP, C:N ratios reached values up to 68, which would imply substantial input of terrigenic material. Such input would be the product of the development of a dense forest canopy around the lake or high runoff from the catchment. However, our record shows Ti concentrations antiphasing

Table 2. Radiocarbon dates for the sediments of Lake Lacandón.

| Depth (cm) | Laboratory ID | Material | Age ($^{14}$C years) | Error (±) |
|---|---|---|---|---|
| 118.25 | Beta-372419 | Pollen extract | 2,060 | 30 |
| 369.27 | Beta-335993 | Pollen extract | 3,380 | 30 |

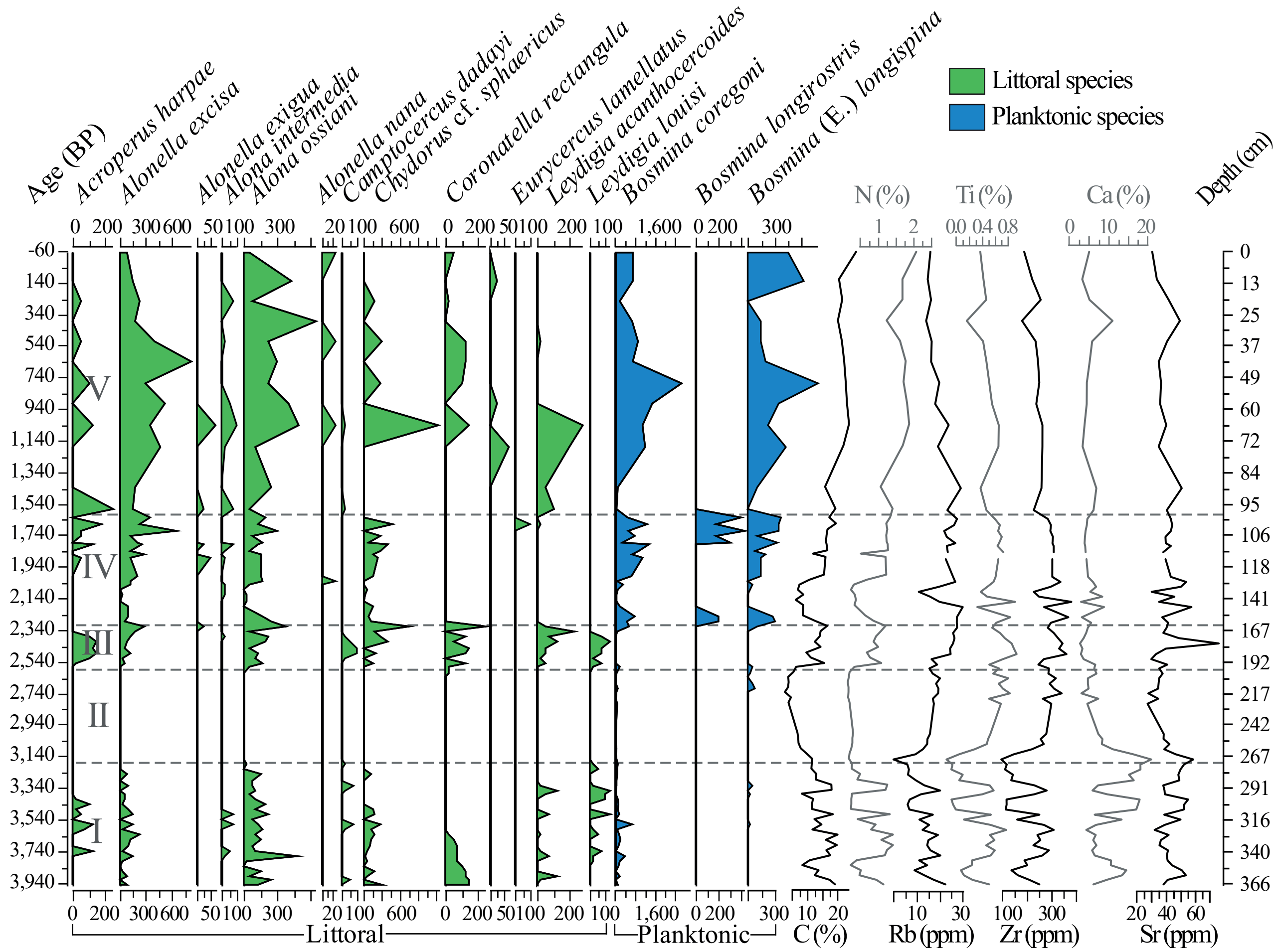


Figure 3. The cladoceran assemblages and geochemical signal of the sedimentary sequence from Lake Lacandón. Cladoceran concentrations in individuals per cm³. Cladoceran habitat preference from Alonso (1996). Cladocera zones are represented by roman numerals superimposed on the abundances of *Acroperus harpae*. Concentrations of C, Ca, N, and Ti are given in weight percentage.

C:N ratios, suggesting that increases in the latter occurred during times of rather dry conditions. It is possible that C concentration during times of drought increased as a result of calcium carbonates precipitation, a process that characterizes dry episodes in the area because of the regional lithology (Hodell *et al.,* 2008). In fact, the correlation between C:N ratios and Ca concentration in the sediments of Lake Lacandón was highly significant (Table 3).

**The temporal evolution of Lake Lacandón**

Cladoceran assemblages through the stratigraphic profile allowed the identification of five time periods, denoted by roman numerals from the bottom to the top of the record, that were characterized by relatively homogeneous environmental conditions (Figures 3, 5, and 6). This zonation of the stratigraphic profile was further supported by the DCA Axis 1 scores (Figure 5) and the lithology of the sedimentary package (Figures 5 and 6). As in pollen analysis, we define a cladoceran zone as a time period characterized by relatively stable biological assemblages, which would in turn reflect relatively uniform environmental conditions (Birks and Birks, 1980). High dynamism is an implicit characteristic of most biological associations, and transitions between environmental states are rarely discrete (Delcourt and Delcourt, 1991). However, we discretized the environmental history to facilitate the description and understanding of environmental settings reflected in our sedimentary record.

Zone I (from the bottom of the record to 275 cm below lake floor, ~3,950 to 3,200 BP) was characterized by an assembly dominated by littoral cladoceran species (Van Damme and Eggermont, 2011), mainly *Alona ossiani, Chydorus* cf. *sphaericus,* and *Acroperus harpae* (Figure 3). These species are known for their tolerance to acidic pH levels and low concentrations of dissolved oxygen in the water (Alonso, 1996; Lotter *et al.,* 1998). They are usually pioneers in early stages of lake development, representing the first species to invade/colonize unoccupied or heavily modified environments (Zawisza and Szeroczyńska, 2007). Thus, this zone probably represents the early stages of the formation of the lake or its recovery from a total dry out. In any case, high variability of species abundance was probably associated with unstable environmental conditions and a primary successional process. Indeed, this time period was characterized by highly variable scores of DCA Axis 1 (Figure 5), although the scores remained in the positive extreme of the axis. The evidence points to a small and shallow lake with abundant macrophytes covering most of its extension.

Ca and Ti concentrations through Zone I suggest that this time period was characterized by a general drought with three wet intermissions: at the bottom of the record, between ~3,750 and 3,550 BP, and at ~3,350 BP (Figure 6). These wet episodes were evidenced by peaks of Ti antiphasing low concentrations of Ca, indicating high erosion levels (Haug *et al.,* 2001) and low precipitation of carbonates (Hodell *et al.,* 1995), respectively. Dry conditions have been reported

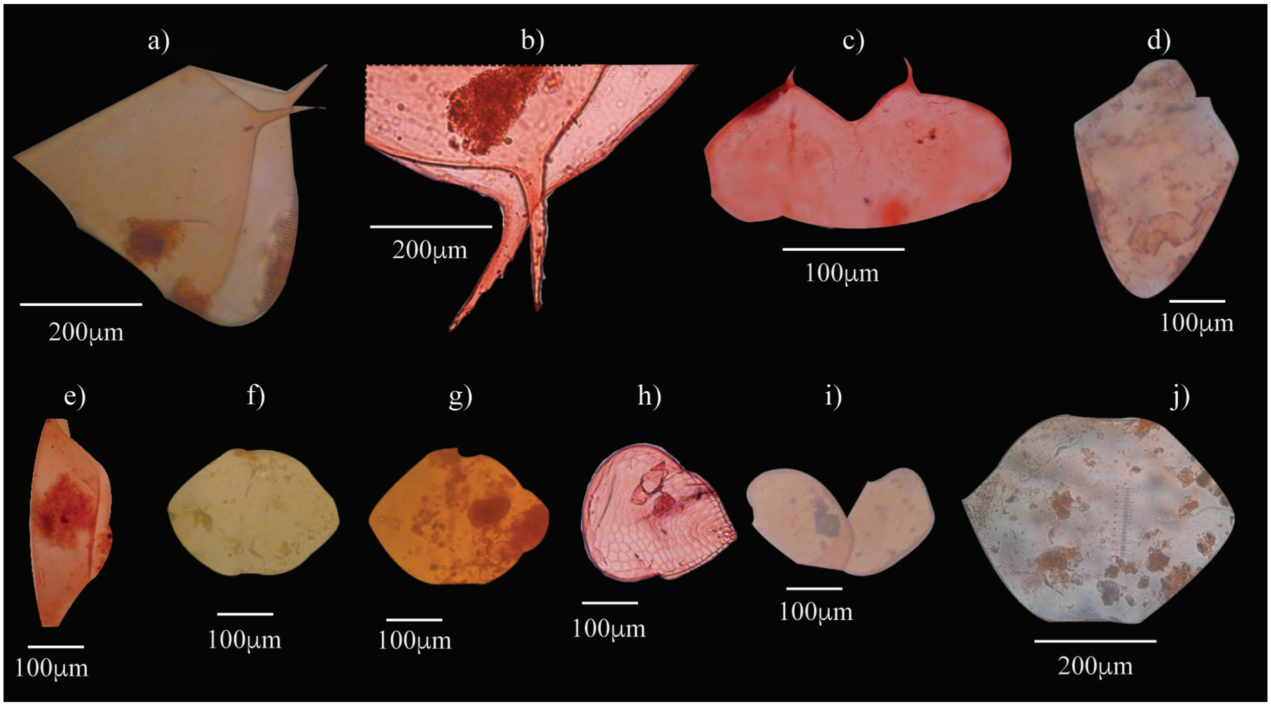


Figure 4. Body parts of the most representative Cladocera taxa found in the sedimentary record of Lake Lacandón. An individual size scale is shown for each photograph. a) Shell of *Bosmina coregoni*. b) Shell of *Bosmina* (*E.*) *longispina*. c) Shell of *Bosmina longirostris*. d) Headshield of *Eurycercus lamellatus*. e) Headshield of *Leydigia acanthocercoides*. f) Headshield of *Alona intermedia*. g) Headshield of *Coronatella rectangula*. h) Headshield of *Graptoleberis testudinaria*. i) Shell of *Chydorus* cf. *sphaericus* J. Headshield of *Leydigia acanthocercoides*.

for the Yucatan Peninsula from ~4,500 to 3,000 BP, with special note of a particular drought that took place at 3,500 BP (Mueller *et al.,* 2009; Carrillo-Bastos *et al.,* 2010), suggesting dry conditions were of regional nature. Indeed, records from the northern Neotropics suggest that the drought that characterized this time period had hemispheric scope (*e.g.*, Curtis *et al.,* 1999; Haug *et al.,* 2001; Tedesco and Thunell, 2003). Particularly, our Ti and Ca records seem synchronous with the high frequency variability of the Ti record from Cariaco Basin, northern Venezuela (Figure 6). It is probable that dry conditions and/or intensive human occupation were associated with relatively open vegetation (*e.g.*, Curtis *et al.,* 1998; Mueller *et al.,* 2009), causing higher erosion during time intervals associated with wetter regional climates (Anselmetti *et al.,* 2007).

Zone II (275 to 200 cm below lake floor, ~3,200 to ~2,600 yr BC) was almost entirely barren of cladocerans. The only species found was *Bosmina* (*E.*) *coregoni* with abundances lower than 150 individuals (Figure 3), making interpretations based on the biological evidence unreliable. The high content of sands and silts in the sediments, and increases of Ti concentration (Figure 6) suggest a high pluvial erosion level of the basin. Indeed, the layer of fine sands between 270 and 250 cm blf could have resulted from a high water of river Nahá that runs only a few tens of meters from Lake Lacandón. According to palynological evidence from the Yucatan Peninsula, the regional vegetation showed a trend towards the dominance of disturbance and open taxa from ~4,500 to 3,000 BP (Curtis *et al.,* 1998; Anselmetti *et al.,* 2007; Mueller *et al.,* 2009). This vegetation change was likely regional in nature, leading to soils more exposed to the erosive power of rainfall. Thus, when relatively humid regional conditions returned at ~3,000 BP, they produced high erosion levels in the basin of Lake Lacandón, producing the layers of rather coarse material that characterized Zone II.

Zone III (200 to 162 cm below lake floor, ~2,600 to ~2,300 BP) was characterized by a total dominance of littoral Cladocera species in a matrix of organic mud (Figure 6). DCA Axis 1 scores suggest extremely low lake levels, which together with high concentrations of C offer evidence of the initial stages of lake development. These attributes are very similar to those found in the bottom of the record, and the zone probably represents the starting of a primary successional process of recolonization following what seems to have been a major disturbance in Zone II. High and low concentrations of Ti and Ca suggest the inception of relatively wet conditions after the environmental instability that characterized zones I and II. The Cariaco Basin Ti record shows a progressive decrease of moisture in the northern Neotropics through the Holocene, with specially dry and variable conditions between 4,000 and 2,400 BP (Haug *et al.,* 2001). This anomaly in the progressive trend was probably the result of an intensification of the El Niño activity (Moy *et al.,* 2002), which was also probably responsible for part of the environmental instability expressed in zones I and II of our record. The evident establishment of conditions that favored the recovery of the cladoceran community in Lake Lacandón was probably the result of the stabilization of regional conditions after the aforementioned dry period.

Zone IV (160 to 100 cm below lake floor, ~2,300 to ~1,600 BP, Figure 3) was characterized by an increase of planktonic species in the cladoceran communities, showing a trend towards a larger lake with open water areas. This expansion and therefore slight deepening of the lake was likely result of higher moisture availability evidenced in high Ti concentrations (Figure 6). *Bosmina longirostris*, a specie associated with high trophic levels (Bērzinš and Bertilsson, 1989), dominated the planktonic component of the cladoceran assemblages in the upper part of the zone. Additionally, C and N increased whereas C:N ratios and Ca concentrations remained stable, evidencing an authigenic provenance of the C in the sediments. Thus, this time period was characterized by a highly-productive enlarging deepening lake. Relatively wet conditions have been reported during this time period for the Yucatán Peninsula

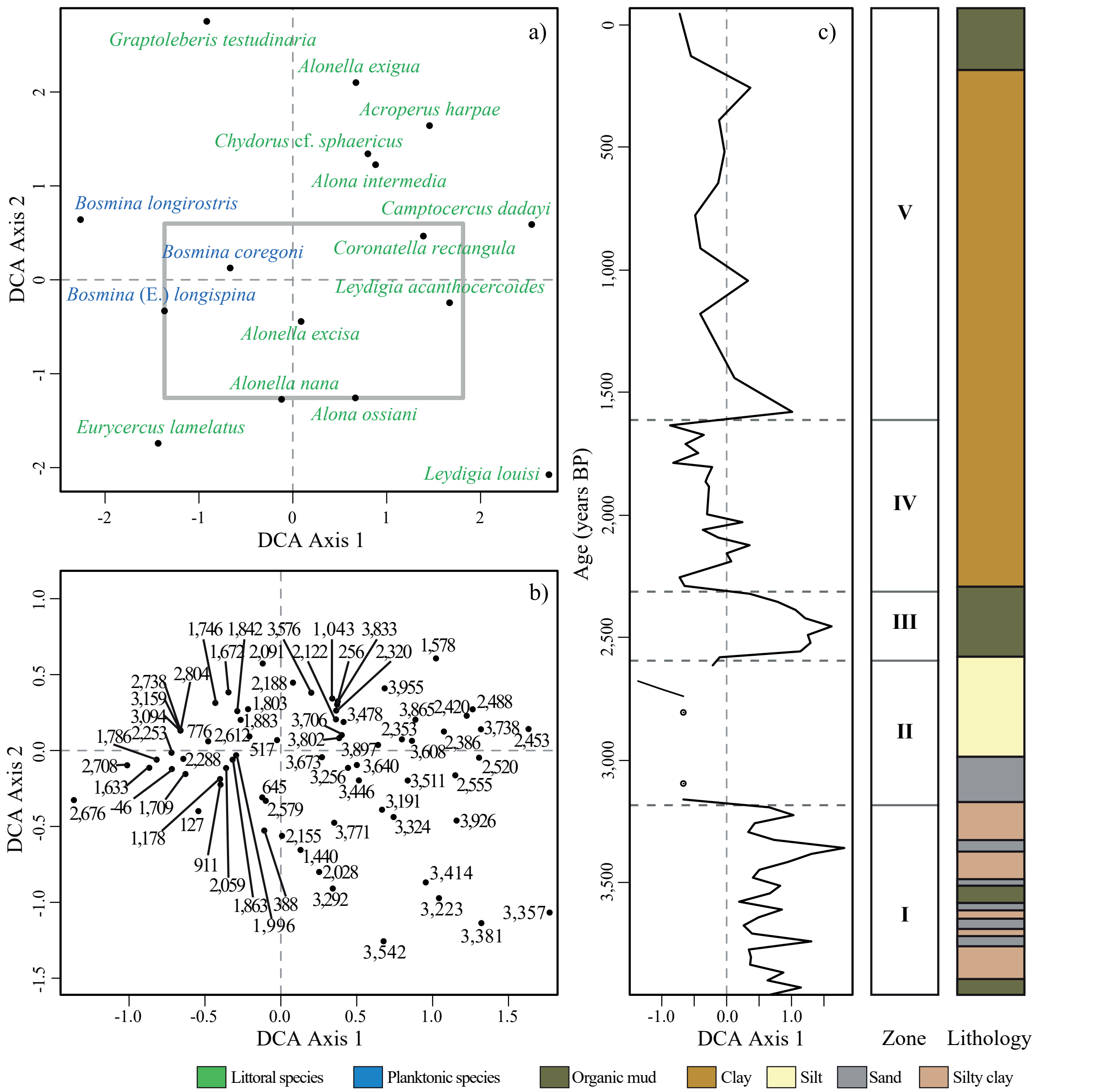


Figure 5. Detrended Correspondence Analysis (DCA) of the cladoceran assemblages of the sedimentary sequence from Lake Lacandón. a) Species ordination, with the gray rectangle showing the space occupied by samples (panel b). b) Samples ordination; each samples was labeled with the age derived from the chronological model. c) Axis 1 sample scores along age. The columns on the left and right sides show Cladocera zones and lithology, respectively.

(Curtis and Hodell, 1996; Mueller *et al.,* 2009; Carrillo-Bastos *et al.,* 2013), implying a regional pattern of mild climatic conditions.

Zone V (from 100 cm below lake floor to mud-water interface, the last ~1,600 years) was characterized by contrasting trends in the cladoceran community and the Ti concentrations (Figure 3). The cladoceran community has been progressively enriched in planktonic components, which together with a decreasing trend of DCA Axis 1 scores implies a general increasing in lake level (Figure 6). Insolation seasonality at the latitude where Lake Lacandón lies has been decreasing through the last 4,000 years (Figure 6), with decreasing and increasing summer-fall and winter-spring insolation, respectively (Berger and Loutre, 1991). The decrease of summer insolation, directly associated with summer rainfall given the seasonal northern position of the

Table 3. Pearson correlation for the analyzed elements. Highly significant correlations ($p$-value < 0.005) shaded in grey. Significance levels were corrected for family-wise error.

| $r_p$ | N | C:N | Ca | Rb | Sr | Ti | Zr |
|---|---|---|---|---|---|---|---|
| **C** | 0.93 | -0.46 | -0.18 | 0.17 | 0.01 | -0.03 | -0.14 |
| **N** | | -0.70 | -0.50 | 0.41 | -0.21 | 0.29 | 0.19 |
| **C:N** | | | 0.87 | -0.73 | 0.43 | -0.76 | -0.71 |
| **Ca** | | | | -0.78 | 0.55 | -0.93 | -0.89 |
| **Rb** | | | | | -0.12 | 0.74 | 0.81 |
| **Sr** | | | | | | -0.50 | -0.39 |
| **Ti** | | | | | | | 0.96 |

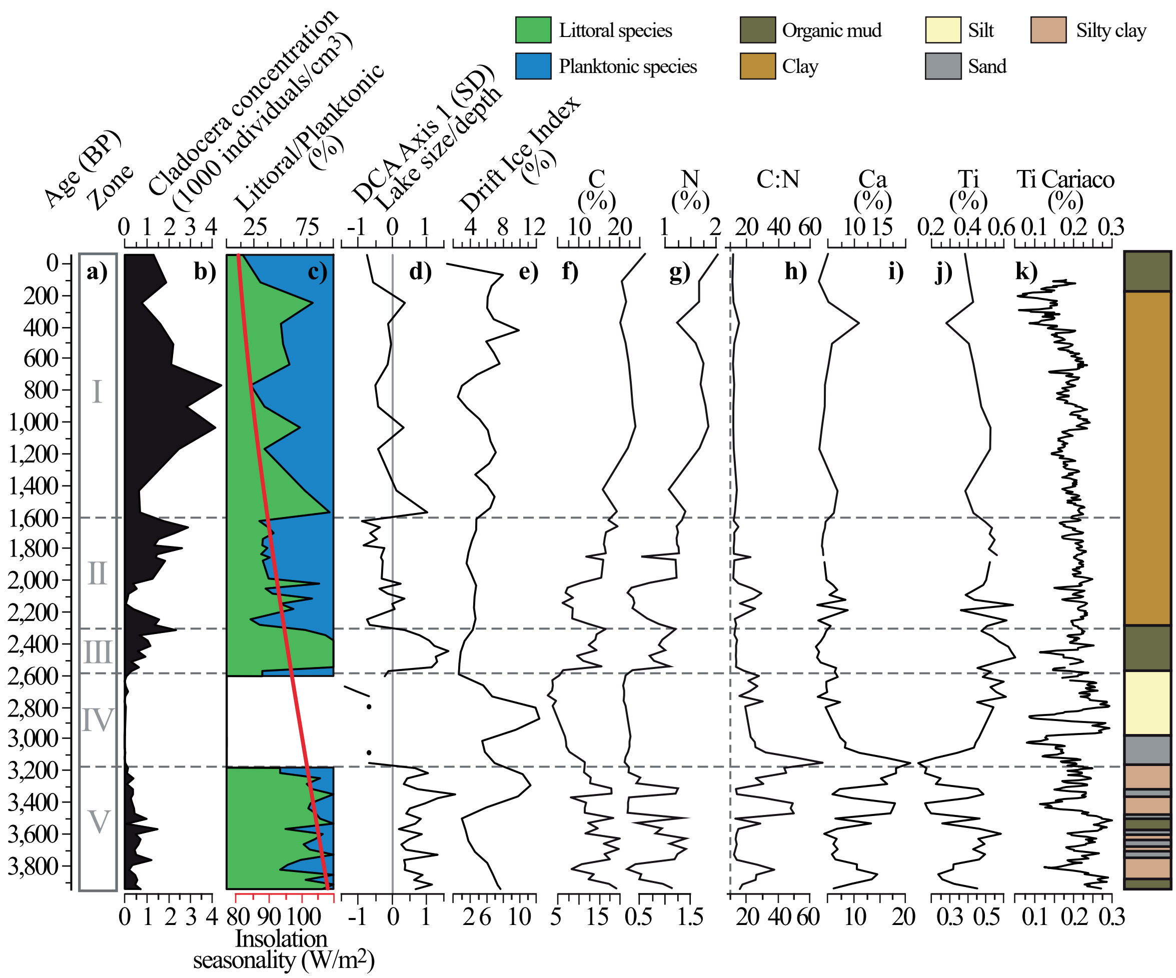


Figure 6. The environmental history from the sediments of Lake Lacandón. a) Cladocera zones; b) cladoceran concentration, number of individuals per cm$^3$; c) percentage of littoral and planktonic cladoceran species (environmental affinities from Alonso, 1996), and insolation seasonality (summer – winter, in red) (insolation data from Paillard *et al.,* 1996); d) Detrendend Correspondence Analysis, Axis 1 sample scores in standard deviations (SD) plotted in time as representative of relative lake size/depth; e) percentage of lithic grains in the sediments of the North Atlantic (Bond *et al.,* 2001); f-g) carbon and nitrogen weight percentages, respectively; h) C:N ratios, with the dashed vertical line indicating a value of 10; i-j) calcium and titanium concentration, in weight percentage, in the sediments of Lake Lacandón; k) titanium weight percentages, in the sediments of Cariaco basin, northern Venezuela (Haug *et al.,* 2001). The column on the right hand side shows core lithology.

Intertropical Convergence Zone, has been associated with diminishing total annual precipitation in the northern Neotropics (Hodell *et al.,* 1995; Haug *et al.,* 2001). This pattern is reflected in the Ti concentration of sedimentary package of Lake Lacandón, which shows a general trend towards a drier climate (Figure 6). However, increasing insolation during the dry season would facilitate advection of water vapor and orographic precipitation causing winter and spring showers. A slight increase of precipitation during months of water deficit (Figure 1) would have a conservative effect on lake water, explaining the increasing trend of lake size in a context of decreasing total annual precipitation.

Several peaks of littoral species dominance through the last 1,600 years suggest episodes of regression to low lakes levels. Interestingly, these peaks showed coincidence with ice rafted deposits in the North Atlantic (Figure 6). Although these peaks have occurred throughout the Holocene (they configure a periodicity known as Bond Cycles, Bond *et al.,* 2001), they seem to manifest in our record only during the last 1,600 years. Increased discharge of cold fresh water in the North Atlantic that were evidenced the oceanic sediments would have caused ralentization of the Atlantic Turnover Circulation, bringing drier than average conditions to the Yucatán Peninsula and adjacent areas (Hodell *et al.,* 2008; Correa-Metrio *et al.,* 2012). These dry episodes were overimposed on the long term drying trend reflected in the decreasing Ti concentrations (Figure 6), a pattern that has been documented in other records from southern Mexico (Bernal *et al.,* 2011). From the bottom of the record to 1,600 BP regional moisture availability was higher given a more northerly position of the Intertropical Convergence Zone (Haug *et al.,* 2001). This pattern probably counteracted precipitation decreases associated with North Atlantic fresh water discharge. It is possible that at ~1,600 BP the regional precipitation reached a level low enough as to allow the ice discharges to manifest in regional lake levels. Nevertheless, the latter statement constitutes a hypothesis that needs further testing.

## CONCLUSIONS

The sedimentary record of Lake Lacandón offers evidence of a complex and highly variable climatic history through the last 4,000 years. Geochemical and biological evidence suggest a mesotrophic water body through the studied time period. Ti concentrations through the stratigraphic profile suggest that erosion, and therefore probably rainfall, in the Lacandón Forest has been closely associated with hemispheric patterns of climatic variability. Our record showed a long-term trend towards lower total annual precipitation that coincides with the southward displacement of the Intertropical Convergence Zone through the Holocene (Haug *et al.,* 2001). Fluctuations in both the composition of the cladoceran assemblages and the concentrations of Ti and Ca suggest a higher-frequency climatic variability possibly associated with periods of intense El Niño activity (Moy *et al.,* 2002) and/or fresh water discharges in the North Atlantic (Bond *et al.,* 2001). Thus, our record highlights the complexity of the environmental evolution of tropical areas, where climates are the result of the confluence of diverse drivers whose relative contribution may change through time and space.

The evolution of the cladoceran community of Lake Lacandón through time suggests a lake that has been growing in size through the last 4,000 years. This pattern seems contradictory with the regional and local trends towards drier conditions through the Holocene (Hodell *et al.,* 1991; Haug *et al.,* 2001). However, it is possible that the decreasing amount of precipitation through the year were offset by a lowered seasonality. Increasing insolation during the dry season would cause advection of moist air from the ocean towards the mountains, where humidity would eventually precipitate given the elevation gradient. Thus, despite regional climatic trends, the sedimentary record of Lake Lacandón reinforces the idea of mountain flanks harboring disjunct climates and sheltering natural populations from rapidly changing climates (Bush, 2002; Correa-Metrio *et al.,* 2014b). Our results call for prioritizing the conservation of mountain flanks because, as pointed by the fossil evidence, they would offer refugia to natural populations during periods of instable climates.

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