Quaternary Research (2021), **101**, 26–36
doi:10.1017/qua.2020.124

Research Article

Ecological turnover in neotropical freshwater and terrestrial communities during episodes of abrupt climate change

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ABSTRACT

The last 85,000 years were characterized by high climate and environmental variability on the Yucatán Peninsula. Heinrich stadials are examples of abrupt climate transitions that involved shifts in regional temperatures and moisture availability. Thus, they serve as natural experiments to evaluate the contrasting responses of aquatic and terrestrial ecosystems. We used ostracodes and pollen preserved in a 75.9-m-long sediment core (PI-6, ~85 ka) recovered from Lake Petén Itzá, Guatemala, to assess the magnitude and velocity of community responses. Ostracodes are sensitive to changes in water temperature and conductivity. Vegetation responds to shifts in temperature and the ratio of evaporation to precipitation. Ostracodes display larger and more rapid community changes than does vegetation. Heinrich Stadial 5-1 (HS5-1) was cold and dry and is associated with lower ostracode and vegetation species richness and diversity. In contrast, the slightly warmer and dry conditions during HS6 and HS5a are reflected in higher ostracode species richness and diversity. Our paleoecological study revealed the greatest ecological turnover for ostracodes occurred from 62.5 to 51.0 ka; for pollen, it was at the Pleistocene/Holocene transition. Future studies should use various climate and environmental indicators from lake and marine sediment records to further explore late glacial paleoclimate causes and effects in the northern neotropics.

Keywords: Northern neotropics, Ostracodes, Pollen, Paleoecology, Heinrich stadials, Ecological change, Detrended correspondence analysis, Aquatic communities, Terrestrial communities, Guatemala

(Received 14 March 2020; accepted 7 December 2020)

INTRODUCTION

High-resolution continental paleoclimate/paleoenvironment data sets that extend into the Pleistocene are rare, especially from the northern neotropics, a region where shallow lakes first developed in the Early Holocene under warmer and more humid conditions (Brenner et al., 1994; Curtis et al., 1998). One exception is Lake Petén Itzá, northern Guatemala, from which an ~400-ka continuous sediment record was collected in 2006 (Kutterolf et al., 2016). More than 1300 m of sediment was recovered from multiple holes at seven sites (PI-1, PI-2, PI-3, PI-4, PI-6, PI-7, and PI-9) (Mueller et al., 2010) (Fig. 1). Drill sites PI-2, PI-3, and PI-6 contained sediments deposited during the last ~85 ka (Kutterolf et al., 2016). Composite core PI-6 (core length = 75.9 m) from 71 m water depth displayed the highest average recovery (94.9%) and was selected for analysis (Mueller et al., 2010).

The last glacial cycle in northern Central America was characterized by alternating periods of dry and wet conditions, identified in the sediment record of Lake Petén Itzá as layers of gypsum and clay, respectively (Hodell et al., 2008). Thick gypsum layers are associated with Heinrich events in the North Atlantic (Mueller et al., 2010). During Heinrich stadials, the sudden onset of prolonged cold and dry phases in the northern neotropics was related to progressive cooling of the North Atlantic in response to ice-sheet collapse and enhanced iceberg calving, with massive deposition of ice-rafted debris (Heinrich, 1988; Hemming, 2004; Sanchez Goñi and Harrison, 2010) and a more southerly position of the Intertropical Convergence Zone (Peterson et al., 2000; Cohuo et al., 2018). Such abrupt cooling, along with increases in the ratio of evaporation to precipitation (E/P) and associated

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Cite this article: Pérez L *et al* (2021). Ecological turnover in neotropical freshwater and terrestrial communities during episodes of abrupt climate change. *Quaternary Research* **101**, 26–36. https://doi.org/10.1017/qua.2020.124

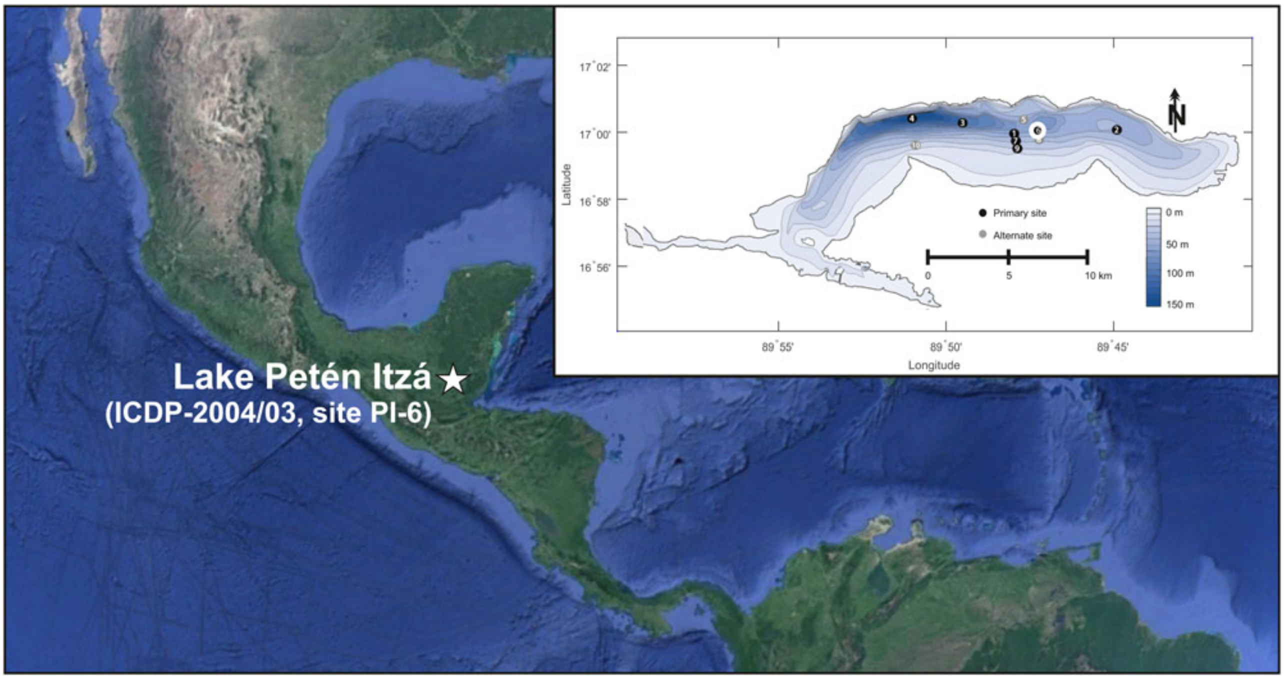

Figure 1. (color online). Location of Lake Petén Itzá (International Continental Scientific Drilling Program Project ID: ICDP-2004/03, site PI-6) (modified from Google Earth, 2020); the bathymetric map of Lake Petén Itzá shows the location of the primary (black) and alternate (gray) coring sites; the white circle is the location of site PI-6 (modified from Hodell et al., 2008).

shifts in lake variables (water level, conductivity), had a profound influence on glacial-age aquatic and terrestrial biota in the northern neotropics. Previous studies show that fluctuations in relative abundances of ostracode species during the intervals 53–14 ka (PI-2, collected from 54 m water depth; Cohuo et al., 2018), 24–10 ka (PI-6, collected from 71 m water depth; Pérez et al., 2011a), and in the Late Holocene (cores PI–SC-1and PI–SC-2, collected from 10 m and 40 m water depth, respectively; Pérez et al., 2010a) reflected shifts in past lake stage and water conductivity (Fig. 1). Cohuo et al. (2018) demonstrated that climate and environmental conditions differed among Heinrich Stadial 5a (HS5a) and HS1, previously described simply as “cold and dry.” They used biological and nonbiological variables to describe the detailed structure of each stadial and identified four different types of climatic conditions. Information on how neotropical aquatic communities responded to climate variability from 85 to 52 ka, however, is still lacking.

The above studies, and similar ones undertaken elsewhere, used the traditional approach of assessing past shifts in species composition and relative abundance, but did not quantify the magnitude and velocity of changes in freshwater communities in response to climate and environmental changes (e.g., Cohen et al., 2007; Wagner et al., 2009). Paleoecological studies of terrestrial vegetation in the northern neotropics have been subject to such analyses (Correa-Metrio et al., 2012a, 2012b), and as noted by Correa-Metrio et al. (2014a), multivariate methods can be applied to fossil counts from both terrestrial and freshwater ecosystems to quantify community responses and determine the magnitude and velocity of ecological change. Detrended correspondence analysis (DCA) enables the quantification of ecological change from fossil data sets. Additionally, given successive standardizations of the data set (Hill and Gauch, 1980), the new space is defined by axes expressed in terms of standard deviations (SDs). Distances among samples in the newly ordinated space are also expressed as SDs, enabling the quantification of ecological change in the fossil record (Correa-Metrio et al., 2014a). Estimates of rates of ecological change can then be determined by dividing the ecological distance between two samples by the number of years between their times of deposition (Correa-Metrio et al., 2012b). This quantitative historical perspective yields information about species ecology and sensitivity to climate and environmental changes that cannot be gleaned from modern studies of lakes alone. Moreover, DCA-based quantification enables reliable comparisons of the magnitudes and velocities of biological responses of aquatic and terrestrial species, communities, and ecosystems over different time scales (e.g., millennia, centuries, decades) and calculation of the time required for biotic recovery after environmental disturbance (Correa-Metrio et al., 2014a).

Ostracodes and pollen are the most abundant and well-preserved microfossils in the sediments of karst lakes in the northern neotropics (Pérez et al., 2011a; Correa-Metrio et al., 2012a, 2012b; Díaz et al., 2017). Their combined study represents a powerful approach because they display complementary environmental sensitivities and together provide insights into aquatic and terrestrial biotic changes during the late Quaternary. Ostracodes (Crustacea: Ostracoda) are sensitive indicators of environmental change in freshwater ecosystems. Their communities respond rapidly, in part because individuals have short life cycles (Pérez et al., 2010a). Ostracodes in lake sediment cores have been used to infer past shifts in lake stage and water-column conductivity, temperature, pH, trophic state, and ionic composition (Pérez et al., 2013a, 2013b; Cohuo et al., 2020). Their use in climate and environmental inferences is maximized by combining molecular, morphological, and ecological approaches (Macario-González et al., 2018).

Pollen is one of the most studied terrestrial bioindicators in paleoenvironmental research and can be used to track the response of terrestrial vegetation to past climate and environmental changes, although shifts in pollen rain may lag those changes if, for instance, it takes time for taxa to migrate or reach maturity (Correa-Metrio et al., 2014a). Pollen grains are used to explore the influence of temperature, rainfall, and humans on past vegetation (Correa-Metrio et al., 2014a; Franco-Gaviria et al., 2018). Inferences about the magnitude and velocity of past vegetation change, however, are complicated mostly by differences of pollination mechanisms (aerophilous vs. zoophilous), which result in different pollen production rates and dispersal capabilities (Leyden, 2002).

Despite the potential promise of studying aquatic invertebrate remains and pollen in combination, few studies have compared climate-driven changes in freshwater and terrestrial communities simultaneously; i.e., in lakes and their catchments, especially at sites in the northern neotropics (Lozano-García et al., 2010; Correa-Metrio et al., 2014a). Studies that compare responses of freshwater and terrestrial bioindicators are important and provide more robust insights into past climate and environmental conditions because they yield multiple independent lines of evidence that can be compared.

One challenge associated with studying remains of a single taxonomic group in lake sediments is microfossil preservation. For instance, a decline in sediment pH, resulting from a change in lithology and/or organic matter degradation, might cause carbonate shell dissolution, thereby modifying or even eliminating a component of the fossil record (Leyden, 2002; Pérez et al., 2010a). Multiple microfossil taxonomic groups that are composed of different materials (e.g., carbonate, chitin, silica, sporopollenin) can complement one another and be used to assess internal consistency of the fossil record. Additionally, the environmental sensitivity of different taxonomic groups and their ecological interactions can be explored (Correa-Metrio et al., 2014b).

Evidence of climate and environmental changes associated with Heinrich events is preserved in multiple geoarchives around the world, including, among others, stalagmites from China (Dong et al., 2018), marine sediments in the North Atlantic (Heinrich, 1988; Elliot et al., 2002; Sanchez Goñi and Harrison, 2010), and some lake sediments (Grimm et al., 2006; Lozano-García et al., 2015). As noted above, the sediment record from ancient Lake Petén Itzá provided an opportunity to investigate past climate variability in the lowland neotropics and its effects on aquatic and terrestrial biota (Correa-Metrio et al., 2012a; Cohuo et al., 2018).

Pollen-based evidence for climate-driven changes in vegetation during the last ~85 ka shows that terrestrial ecosystems in the region were relatively resilient, although plant associations without modern analogs were common after abrupt climate changes (Correa-Metrio et al., 2012a, 2012b). Nevertheless, high-resolution information about biotic changes in the aquatic ecosystem were limited to the last ~54 ka (Pérez et al., 2011a, Cohuo et al., 2018) and were derived from cores collected at different sites (PI-2, PI-6), precluding comparison of the aquatic and terrestrial records over the last 85 ka. The well-dated long core from site PI-6 was chosen to compare past changes in ostracode and vegetation communities. Previous studies of pollen (Correa-Metrio et al., 2012a, 2012b) and ostracodes (Pérez et al., 2011a) from the PI-6 record relied on an age model in Hodell et al. (2008), which was updated by Kutterolf et al. (2016) and is used here.

We identified and enumerated ostracode remains in previously unanalyzed samples from core PI-6 and together with previously analyzed pollen (Correa-Metrio et al., 2012a) quantified the effects of abrupt climate and environmental shifts on freshwater ostracode and terrestrial plant communities in northern Guatemala over the past 85 ka by estimating the magnitude and velocity of ecological change. We addressed the following questions: (1) What were the main environmental variables that shaped glacial-age aquatic ostracode and terrestrial vegetation communities? (2) How strongly and how rapidly did freshwater and terrestrial communities respond to abrupt climate and environmental changes, and was HS6-1 associated with higher-magnitude and rapid responses? (3) What conditions characterized aquatic and terrestrial ecosystems between 85 and 53 ka?

MATERIALS AND METHODS

Study area

Lake Petén Itzá (17°0′N, 89°51′W; 110 m asl) is a closed-basin lake and the largest (~100 km^2) and deepest (~160 m) water body in the karst lowlands of Guatemala (Fig. 1) (Pérez et al., 2011b). The catchment covers ~1064 km^2 (Méndez and Pinelo, 2008). The region is characterized by a relatively humid tropical climate, with mean monthly air temperatures ranging from 22.3°C in January to 29.8°C in May. Mean annual rainfall is ~1601 mm, with the dry season typically extending from about late December to early May and the rainy season from later in May through early December (Deevey et al., 1980). Lake Petén Itzá has held water continuously for >400 ka (Kutterolf et al., 2016). The Lake Petén Itzá Scientific Drilling Project recovered 1327 m of sediment from the basin in 2006, using the GLAD800 drill rig. Cores were collected at seven drill sites (Fig. 1), with multiple holes drilled at most of them (Mueller et al., 2010).

Sedimentology and age model for core PI-6

A 75.9-m-long composite sediment sequence from three holes (PI-6, ~85 ka) was recovered from a water depth of 71 m and subsampled at the LacCore facility, University of Minnesota, Minneapolis, USA. The mineralogical composition of the sediments was reported in Mueller et al. (2010). The updated core chronology was developed using 44 AMS ^{14}C dates on terrestrial organic matter and the presence of six volcanic ash layers with known ages (Kutterolf et al., 2016). Radiocarbon dates were calibrated using Intcal09 (Reimer et al., 2009).

Biological analysis

Two 1-g aliquots were sampled every ~20 cm along the length of the core for ostracode analysis. One aliquot was used to determine sediment percent dry weight, whereas the other was wet-sieved (63 µm). For the latter, sediments were gently disaggregated with freeze/thaw cycles, and if this was unsuccessful, 3% H_2O_2 was used (Pérez et al., 2011a). Adult and juvenile valves and carapaces were extracted using fine brushes under a Leica MZ 7.5 stereoscope. Ostracode abundances (adults, juveniles [all larval stages]) are expressed as valves per gram dry sediment. Fossil ostracode identification followed Pérez et al. (2010b) and Cohuo et al. (2017). Ostracode abundances for the interval 24–10 ka were presented in Pérez et al. (2011a), and here we extend that record to 85 ka. Pollen methods and details of the 85-ka pollen record from Lake Petén Itzá are in Correa-Metrio et al. (2012a). We used selected taxa (the most representative for the following periods: >53 ka, HS6-1, late Pleistocene/Holocene transition, and Holocene) from the pollen record (Correa-Metrio et al., 2012a) to explore changes in vegetation over the past 85 ka.

Heinrich stadial chronozones follow Cohuo et al. (2018) and Sanchez Goñi and Harrison (2010).

Statistical analyses

We selected DCA over other multivariate techniques to evaluate ecological turnover of both the ostracode and the vegetation communities during the past 85 ka. DCA was also chosen because it is well suited for summarizing past ecological change, relies on few assumptions, and has the advantage that results can be used to assess ecological turnover. Moreover, multidimensional-rescaling techniques (e.g., principal components analysis and correspondence analysis) assume linearity of species response to environmental gradients, leading to unbalanced ordinations, and biases in identification of environmental gradients (Hill and Gauch, 1980; Correa-Metrio et al., 2014a). The pollen-based DCA was previously reported (Correa-Metrio et al., 2012a, 2012b), but used an outdated age model. Here, both the pollen- and the ostracode-based DCAs were run using an updated version of the core chronology.

DCA species scores (adult and juvenile ostracodes, pollen) along the first two DCA axes were used for environmental interpretation of the new ordinated space. Interpretation of the ordination biplot of freshwater and terrestrial taxa was based on modern ecological information derived from training sets in the region, across a precipitation transect (Correa-Metrio et al., 2011; Pérez et al., 2011b, 2013b).

Euclidean distance among samples, based on DCA scores, was used to estimate magnitude and rate of ecological change, following Correa-Metrio et al. (2014a). Data processing was performed using the R package vegan, version 2.5-6 (Oksanen et al., 2019). Given that DCA scores are expressed as SDs, Euclidean distances represent differences in composition and structure in ostracode and pollen assemblages. Thus, the distance between samples can be interpreted as quantiles of a normal distribution, with the cumulative probability representing ecological turnover. Consequently, a distance of 1 SD between two samples represents 38% of ecological turnover in terms of the analyzed assemblage; 2 SDs represent a turnover of ~68%; and 4 SDs represent an ecological turnover of ~95% (Zar, 1999). The velocity of ecological change was determined by dividing the distance between two adjacent samples by the time elapsed between them. Shannon-Wiener diversity indices (Magurran, 2004) were calculated using the relative abundances of ostracode and pollen taxa in the samples.

RESULTS

Species richness, relative abundance, and diversity of freshwater and terrestrial communities in long core PI-6

Nine ostracode species were identified in core PI-6 from Lake Petén Itzá. *Paracythereis opesta* (Brehm, 1939), *Pseudocandona antilliana* Broodbakker, 1983, *Cytheridella ilosvayi* Daday, 1905, and *Darwinula stevensoni* (Brady and Robertson, 1870) are benthic taxa, whereas nektobenthic species include *Cypria petenensis* Ferguson et al., 1964, *Cypridopsis vidua* (Müller, 1776), *Heterocypris putei* (Furtos, 1936), *Strandesia intrepida* Furtos, 1936, and an unidentified species that belongs to the family Cyprididae, which we named Cyprididae sp. 1. Endemic species *P. opesta* and *C. petenensis* have been present in the lake for the past 85 ka (Fig. 2). The greatest number of species identified in a sample was seven, at 83.5, 59.8, 46.8–45.4, and 41.3 ka. A decrease in ostracode species richness occurs after ~45.5 ka. The highest Shannon-Wiener diversity index value (H = 1.29) was calculated for adult ostracodes at 41.0 ka and for juvenile ostracodes (H = 1.69) at 60.8 ka. Diversity index values for adult and juvenile ostracodes displayed different temporal trends. Adult diversity was high between ~50.0 and 10.0 ka, with a decline between HS3 (~32.7–31.3 ka) and HS2 (~27.6–23.2 ka). Juvenile diversity was high during HS6 (~63.2–60.1 ka) and HS5a (~53.0–52.0 ka), low during HS5 (50.0–47.0 ka) and HS4 (~40.0–38.1 ka), and then remained low until ~32.5 ka, after which it increased until HS1 (~17.5–14.8 ka). Abundances of ostracodes were relatively low and were often absent between 80.0 and 50.7 ka. Juveniles of *C. petenensis* dominated during that period. Thereafter, and for the rest of the Pleistocene, abundances were higher, with alternation between dominance of *P. opesta* and *C. petenensis*. The ostracode *C. ilosvayi* was found sporadically, with higher abundances in the interval 61.8-45.4 ka and during the Late Holocene, at 2.8 ka.

Juvenile ostracodes were generally more abundant than adults (Fig. 2). The highest concentration of juvenile valves was found at 36.5 ka BP, whereas adult valves were present in higher concentrations later in the Pleistocene and in the earliest Holocene, at 13.7, 13.4, and 10.7 ka BP. *C. petenensis* showed an abrupt decline in abundance during all HS, which were characterized by two different species assemblages. HS6 and HS5a were characterized by low abundances of *C. ilosvayi* and Cyprididae sp. 1, whereas the other stadials possessed ostracode taxa *H. putei* and/or *S. intrepida*. *C. vidua* and *P. antilliana* were present in all stadials. Species richness, and adult and juvenile diversity, generally dropped slightly during most stadials; the exceptions are HS6 and HS5a (Fig. 2).

The pollen record was described by Correa-Metrio et al. (2012a), and here we highlight the most important findings to facilitate understanding of the comparison between freshwater and terrestrial communities. A total of 177 pollen types were identified, and the number of taxa in each sample ranged between 12 and 60. The Shannon-Wiener diversity index ranged from 0.84 to 3.46 and displayed low values during most Heinrich stadials and the Pleistocene/Holocene transition. *Quercus*, *Pinus*, and Cyperaceae were the dominant taxa during the last glacial, whereas the tropical forest family Moraceae dominated during the Holocene (Fig. 2). From 85.0 to 60.1 ka BP, Melastomataceae was the dominant taxon, but abundances fluctuated. *Myrica* and *Quercus* increased slightly toward HS6 and showed an abrupt decline around that time. From 61.7 to 48.7 ka, a pine savanna dominated the regional vegetation, whereas from 48.7 ka to the end of the glacial, vegetation was dominated by *Pinus-Quercus* forests. Taxa that showed a negative response (low abundances) (0–62%) during the stadials included *Ambrosia*, Melastomataceae, *Myrica*, *Pinus*, and *Quercus*, whereas a positive response (higher abundances) was evident for Poaceae. Cyperaceae maintained low abundances during the stadials, yet displayed systematic ephemeral abundance peaks and was especially abundant at the end of each one (Fig. 2).

Detrended correspondence analysis of the ostracode and pollen records

Species scores for adult and juvenile ostracodes showed a clear pattern of environmental preference through DCA axis 1 (Fig. 3), whereas distribution along axis 2 was difficult to interpret. Thus, environmental interpretation of the ostracode-based

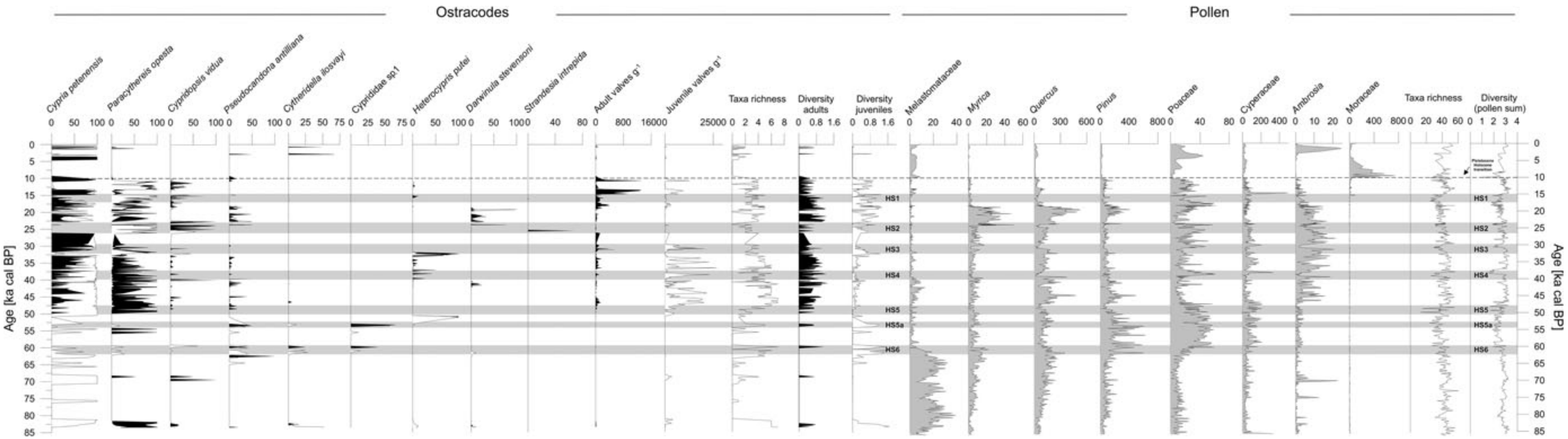

Figure 2. Left: Relative abundance (%) of fossil ostracode species assemblages in PI-6 (black = adults, white = juveniles); the dominant species *Cypria petenensis* and *Paracythereis opesta* are followed by the less abundant species *Cypridopsis vidua* and *Pseudocandona antilliana* and the less frequent species (*Cytheridella ilosvayi* to *Strandesia intrepida*); adult valves g^{-1} = total adult valves in 1 g dry sediment; juvenile valves g^{-1} = total juvenile valves in 1 g dry sediment; taxa richness = number of species; diversity adults = Shannon-Wiener diversity index based on adult counts; diversity juveniles = Shannon-Wiener diversity index based on juvenile counts. Right: Selected pollen taxa in appearance and dominance order in the PI-6 record. Percentages were calculated based on the pollen sum, which excluded Moraceae, *Pinus*, *Quercus*, and Cyperaceae (modified from Correa-Metrio et al. 2012a); Moraceae highlights the Pleistocene-Holocene transition; taxa richness = total number of taxa; diversity (pollen sum) = Shannon-Wiener diversity index based on pollen sum. The horizontal gray bars indicate Heinrich Stadial 6-1 (HS6-1), the dashed line marks the Pleistocene-Holocene transition.

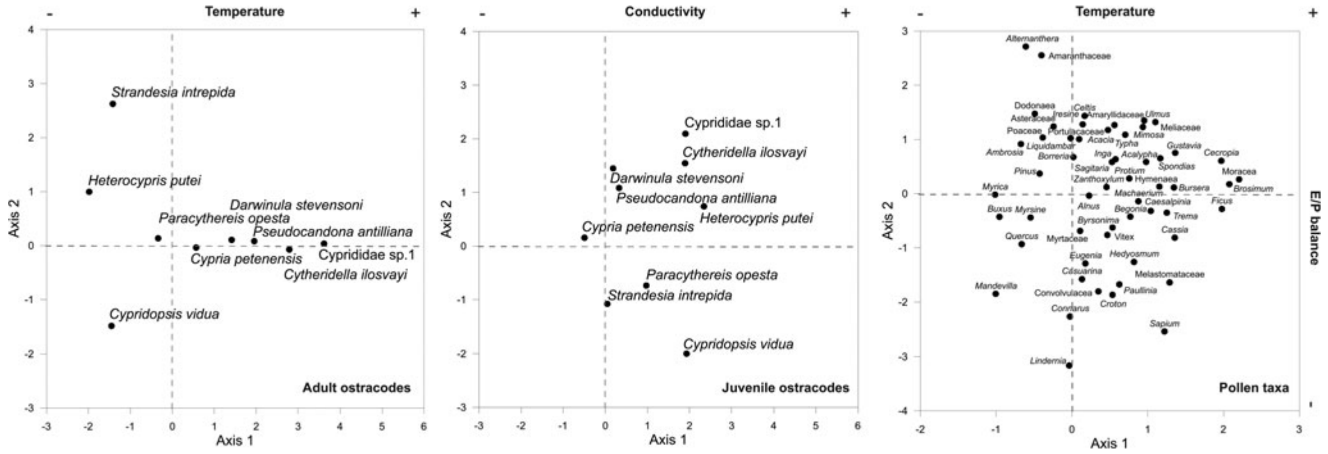

Figure 3. DCA species scores of axes 1 and 2 for adult and juvenile ostracodes and pollen in the PI-6 record showing clear patterns of environmental preferences. Modern ecological information (see text for references) suggests that ordination analyses of adult ostracodes relate to a temperature gradient, analyses of juvenile ostracodes relate to water conductivity, and analyses of vegetation (pollen) relate to temperature and the evaporation to precipitation (E/P) ratio.

DCA is based solely on axis 1. For pollen assemblages, both axes were environmentally informative. Ordination biplots were interpreted using modern ecological information available for ostracodes (Pérez et al., 2010b, 2010c, 2011a, 2012, 2013b) and pollen (Correa-Metrio et al., 2011). The ordination of adult ostracodes along axis 1 was related to a temperature gradient. *H. putei* and *P. opesta* (smaller values) are typical ostracode species that tolerate slightly colder temperatures, whereas *C. ilosvayi* and Cyprididae sp. 1 (larger values) prefer higher temperatures. Species scores for juvenile ostracodes relate to a water-conductivity gradient. *C. petenensis* (negative values) is the dominant species during periods when conductivity was low (humid climate), whereas *H. putei* and *C. vidua* (higher values) are species that tolerate higher conductivities and lower lake levels (i.e., a drier climate). Available modern information (Correa-Metrio et al., 2011) suggests that pollen taxa, positioned on axis 1, also follow a temperature gradient. With higher temperatures, montane taxa (e.g., *Myrica*) display lower values, whereas tropical taxa such as Moraceae, *Ficus*, and *Bursera* have higher values.

Inferred patterns of ecological turnover of freshwater taxa and vegetation show contrasting patterns of ecological response to environmental variability (Fig. 4). Ostracodes display a larger range of DCA axis 1 sample scores (-2.0–3.0) than do pollen (-0.6–2.0) (Fig. 4a and b). Higher DCA values for juvenile ostracodes (axis 1) indicate lower lake levels, higher conductivity, and thus drier conditions during HS6-1, except HS4, which was characterized by lower DCA sample scores (Fig. 4a). DCA values for ostracodes suggest higher lake levels (lower conductivity) during most of the Holocene. Pollen DCA values (axis 2) also indicate lower precipitation during all Heinrich stadials. Vegetation surrounding Lake Petén Itzá between 60.1 and 47.0 ka (higher DCA values) likely adapted to dry conditions. For most of the stadials, ostracode response to a drying climate preceded changes in vegetation. Peaks in pollen DCA axis 2 scores were systematically preceded by high ostracode juvenile DCA axis 1 values. Temperature was inferred from changes in the DCA sample scores of axis 1 for both adult ostracodes and pollen (Fig. 4b). Nevertheless, temperature variability was more dynamic in the freshwater record. The major change in the terrestrial record occurred during the Pleistocene/Holocene transition. Most Heinrich stadials show lower DCA values (adult ostracodes), suggesting lower temperatures; the exceptions are HS6 and HS5a, which were characterized by higher temperatures; this was not evident in the pollen record. Slightly higher DCA values (DCA-pollen axis 1, Fig. 4b) before 61.0 ka BP, however, suggest incrementally warmer conditions. Other periods with higher temperatures were also indicated by ostracodes (DCA-adults axis 1, Fig. 4b) at the end of HS2 and during the Late Holocene.

According to estimates of ecological change and its associated rates, the response of the aquatic ecosystem to changes in the E/P balance and temperature was larger (ostracodes: 5.3 SD, pollen: 1.3 SD) and more rapid (ostracodes: 17.2 SD/100 yr, pollen: 0.14 SD/100 yr) than responses calculated using pollen (Fig. 4c and d). Ratios higher than 8 SD/100 yr account for a complete turnover. Ecological turnover in both ecosystems (Fig. 4c and d) was larger during all Heinrich stadials, especially HS5 and HS2. An ecological change in the aquatic ecosystem was especially rapid during HS4, HS3, and HS1 (Fig. 4e). Vegetation response was faster during HS6 and HS2. A major ecological change in the lake environment occurred from ~62.5 to 50.9 ka and was fast at the onset and termination of each stadial. Warmer and drier conditions between ~62.5 and 53.1 ka (Fig. 4a and b) are reflected in the large magnitudes and velocities of change in the ostracode assemblages (Fig. 4c and e).

DISCUSSION

Composition and diversity of freshwater and terrestrial communities in and around Lake Petén Itzá during the past 85 ka

Nine ostracode species were identified in the lake sediment record that spans the last ~85 ka (Fig. 2). Much higher ostracode species richness has been reported from larger and older lakes. For instance, species richness values of ~200 and 100 were reported for Lake Baikal (Russia) and Lake Tanganyika (East Africa), respectively (Martens et al., 2008). A total of 32 living ostracode species were reported for Lake Ohrid (Albania and Macedonia) (Lorenschat et al., 2014). Thus, large and ancient lakes have been identified as biodiversity hotspots. It seems that ostracodes are not great dispersers, although there have been habitat-related endemic radiations via groundwater, temporary pools, and

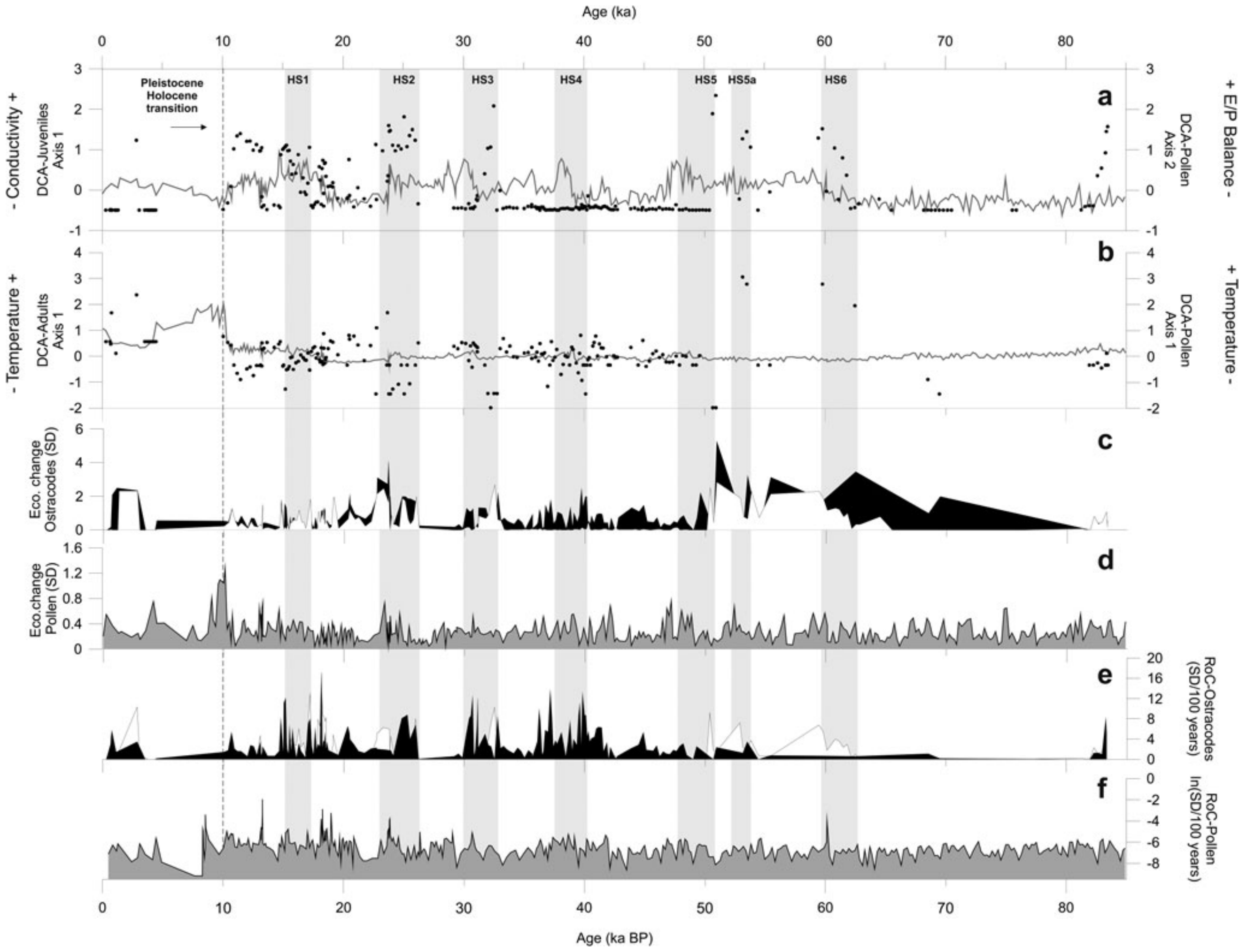

Figure 4. A detrended correspondence analysis (DCA) of the PI-6 aquatic (ostracodes) and terrestrial (pollen) records. Top (a, b): Horizontal stratigraphic plots of DCA sample scores along axes 1 and 2 for adult and juvenile ostracodes and pollen (gray line); DCA values for adult and juvenile ostracodes were plotted as dots because of their scarcity between 85 and 50 ka and during the Holocene; changes in DCA sample scores for juvenile ostracodes (axis 1) and pollen (axis 2) were interpreted as changes in water conductivity and the E/P balance, respectively; changes in DCA sample scores for adult ostracodes (axis 1) and pollen (axis 1) indicate changes in temperature. Middle (c, d): Ecological change for ostracodes (c, adults = black, juveniles = white) and pollen (d, gray) calculated as the Euclidean distance between contiguous samples. Bottom (e, f): Rates of ecological change for ostracodes (e, adults = black, juveniles = white) and pollen (f, gray). The vertical gray bars indicate HS6-1, the dashed line marks the Pleistocene-Holocene transition.

ancient lakes. Continuously varying environmental conditions in Lake Petén Itzá might explain the low ostracode diversity. Northern Guatemala hosts many aquatic ecosystems with different ionic compositions and diverse limnological conditions (Pérez et al., 2011b), which could have served as habitats for ostracodes when conditions in Lake Petén Itzá were unfavorable, although most shallow basins were dry during the late glacial.

Low ostracode species richness values, similar to those in the ~85-ka record from Lake Petén Itzá, were found in other lakes from the northern neotropics (Cohuo et al. 2018, Pérez et al. 2011a), suggesting that species richness in the region has remained low since the late Pleistocene. Pérez et al. (2013b) summarized the biodiversity of 63 neotropical freshwater ecosystems and analyzed the principal groups of phytoplankton and zooplankton/benthos, including diatoms, microcrustaceans (i.e., cladocerans, copepods, ostracodes), and chironomids. The highest ostracode species richness value (10 species) was encountered in lowland karst Lakes Bacalar and Milagros (~1 m asl), Quintana Roo, Mexico. Lake Nahá (830 m asl), in the mid-altitude region of the Lacandon forest, displayed the highest species richness (11 species) among the studied mountain karst lakes of Chiapas, Mexico (Echeverría Galindo et al., 2019). The Holocene record from Lake Ocotalito (920 m asl), Chiapas, Mexico, was also characterized by low species richness (six species) (Díaz et al., 2017). Although these results show that ostracode species richness in northern neotropical lakes is low, a high proportion of endemism is evident (Cohuo et al., 2014, 2016, 2017; Pérez et al., 2015; Sigala et al., 2017). For instance, the Lake Petén Itzá ostracode record is composed mainly of tropical taxa. Moreover, the endemic ostracodes *C. petenensis* and *P. opesta* dominated the species assemblage of the past 85 ka. This suggests that such species were resilient, in agreement with the findings of Cohuo et al. (2020). Other species that displayed lower abundances include *H. putei*, *P. antilliana*, and *S. intrepida*. We found only two widespread species, *C. vidua* and *D. stevensoni*, and the unidentified Cyprididae sp. 1 that inhabited the lake from ~62.1 to 53.2 ka. The taxon was unidentifiable to species level because we found only a few adult valves, and it did not emerge as an extant specimen with well-preserved soft parts during previous sampling campaigns across Guatemala, Belize, and Mexico (Pérez et al., 2011a, 2013b, 2015).

The highest ostracode species richness (seven species) was encountered at 83.5, 46.8–45.4, and 41.3 ka (not during Heinrich stadials), and ostracode occurrences were rather sporadic before ~50 ka. Our record shows a decrease in ostracode species richness toward the present (Fig. 2), which was probably a response to an increase in lake stage (less littoral habitat close to the drill site), especially during the Holocene (Mueller et al., 2010). We also observed episodes of abrupt declines in the total number of species, especially during Heinrich stadials (Fig. 2), which coincided with the response of the terrestrial community; i.e., decreases in the total number of plant taxa and the diversity index.

Because freshwater and terrestrial ecosystems in Guatemala and elsewhere in Central America provided a corridor for the exchange of aquatic and terrestrial taxa between North and South America, we would expect ostracode species richness to be high, but surprisingly this was not the case in this study or in previous investigations (Cohuo et al., 2018, 2020). This highlights the role of abrupt climate and environmental changes in shaping biotic communities in the northern neotropics and the different strategies used by species (adaptation, dispersal, reproduction, etc.) during and after such changes (e.g., HS6-1).

The late Pleistocene was characterized by fluctuating adult and juvenile ostracode abundances, mainly *C. petenensis* and *P. opesta*. The total number of juvenile ostracodes always considerably exceeded that of adults, suggesting taphonomic processes at work, transport of juveniles into deeper waters (Whatley, 1988), or particular environmental conditions that triggered higher egg production by female ostracodes to ensure production of sufficient numbers of offspring and/or higher mortality rates. A detailed taphonomic study of ostracode records from cores taken at multiple sites in Lake Petén Itzá (e.g., adult/juvenile ratio, intact vs. broken shells and carapaces, abundance of all ostracode larval stages), extending into the last glacial period could (1) enable basin-wide interpretation of environmental change, (2) improve our understanding of microfossil transport processes in Lake Petén Itzá, and (3) help distinguish between local and regional environmental changes.

Pollen analysis in core PI-6 revealed fluctuating taxonomic richness, ranging from 12 to 60 taxa per sample, and diversity index values varying from 0.84 to 3.46 (Fig. 2). Some ostracode and vegetation taxa displayed similar stratigraphic changes in abundance, e.g., *P. antilliana* and *Pinus*, and *D. stevensoni* and *Myrica*. Vegetation richness and diversity decreased during all Heinrich stadials. Pollen assemblages revealed major differences between late glacial and Holocene vegetation communities (Correa-Metrio et al., 2012a). Whereas vegetation during the late Pleistocene was dominated mainly by *Quercus*, *Pinus*, and Cyperaceae, tropical taxa such as Moraceae were dominant during the Holocene (Fig. 2). Vegetation from 85.0 to 60.1 ka was dominated by Melastomataceae, while *Myrica* and *Quercus* increased slightly toward HS6. Before HS6, Lake Petén Itzá was surrounded by nonmodern-analog vegetation communities. Correa-Metrio et al. (2012b) inferred *Pinus* savanna landscapes during HS6, which were well established between 61.7 and 48.7 ka and associated with high seasonality of precipitation (Correa-Metrio et al., 2012b). Thereafter, until 19.2 ka, temperate mesic taxa dominated the area, along with low occurrences of seasonal tropical taxa (Correa-Metrio et al., 2012b). During other periods in the last glacial, temperate taxa expanded into the northern Central American lowlands, leading to plant communities that were probably more diverse than the region's modern forests (Correa-Metrio et al., 2012b). Climate and environmental variability seems a plausible explanation for maintaining high biotic diversity in neotropical aquatic and terrestrial ecosystems over the long term. Although transient communities of the past were of low diversity, successive climatic fluctuations prevented competitive exclusion and helped maintain diversity through time.

Paleoecology of freshwater and terrestrial communities during the past 85 ka

DCA on microfossil counts from core PI-6 (Fig. 3), along with *a priori* knowledge from modern calibration data sets for the northern neotropics (Pérez et al., 2011a, 2013a; Correa-Metrio et al., 2011; Echeverría Galindo et al., 2019), revealed that temperature, conductivity, and the E/P balance were the main environmental variables that shaped freshwater ostracode and terrestrial vegetation communities in and around Lake Petén Itzá for the past 85 ka. Vegetation surrounding Lake Petén Itzá was influenced directly by air temperature and rainfall, whereas ostracodes were influenced indirectly by the impact of both climate variables on water column conditions. For instance, an increase in E/P affects vegetation communities directly, but influences ostracodes indirectly through decline in lake level and higher electrical conductivity of lake waters.

We also used DCA to explore different controls on adult and juvenile ostracodes. We compared DCA scores for adult and juvenile ostracodes, and based on modern ecological data and DCA ordination, we discovered that adult ostracodes are more sensitive than juveniles to changes in temperature, whereas juveniles react more strongly to variations in E/P, which controls lake level and water conductivity. Freshwater ostracodes generally display nine molts up to adult stage, and sometimes one or more stages may be omitted. The last molt, from A-1 to adult, occurs when environmental conditions for a species are optimal, and temperature is an important variable in this respect (Horne, 2007; Pérez et al., 2011a). Our DCA and *a priori* knowledge revealed this temperature-dependent shift to adulthood, highlighting the importance of distinguishing between juvenile and adult stages for reliable paleoenvironmental interpretations. Future studies should further explore the reproductive strategies of ostracodes, using remains in long sediment records from ancient lakes, and should focus on the ratios of males/females, sexual/asexual species, and adults/juveniles.

Throughout the ostracode record, an alternation in dominance between nektobenthic *C. petenensis* (a deeper-water taxon) and benthic *P. opesta* (a shallower-water taxon) (Fig. 2) was evident, suggesting abrupt changes in the lake level and related water conductivity (Fig. 3, see juvenile ostracodes). Heinrich stadials are marked by the presence of *P. opesta* and an abrupt decline in the abundance of *C. petenensis*. Previous ostracode evidence from Lake Petén Itzá site PI-2 led to the characterization of HS5a-1 as cold and dry periods in the continental northern neotropics (Cohuo et al., 2018). The presence of tropical ostracode species *C. ilosvayi*, *P. antilliana*, and *P. opesta* during Heinrich stadials indicates, however, that water temperatures were likely only 1–3°C lower than the modern lake temperature (Cohuo et al., 2017, 2018). The ostracode species assemblage

Cypridopsis-Heterocypris-Pseudocandona-Strandesia is characteristic of Heinrich stadials, with the exception of HS6 and HS5a, during which *Cytheridella* and Cyprididae appeared, suggesting a relatively warmer and drier environment (Pérez et al., 2011a). Those periods, ~62.1 and 53.2 ka, possess ostracode assemblages without a modern analog, as they include Cyprididae sp. 1, a taxon we have not found in our regional modern training sets (Pérez et al., 2013b). The sporadic presence of *C. ilosvayi* in glacial-age sediments, deposited from 61.8 to 45.4 ka, was unexpected. The presence of this ostracode species indicates warmer waters (>20°C), and it is widely distributed in the neotropics and abundant in Holocene-age sediments (Pérez et al., 2010b, 2011a, 2012; Cohuo et al., 2017). The interval from 62 to 45 ka BP was the first long period of relatively higher temperatures in the water column during the last glaciation, identified in the Lake Petén Itzá record. Ostracodes are the first climate proxy, either biological or nonbiological, to have revealed this episode of warmer glacial-period temperatures. Nevertheless, ostracode abundance was low during this period, suggesting that inferences should be accepted with caution. Cohuo et al. (2020) found shells of *C. ilosvayi* at 87–85 and 53 ka in drill site PI-2, confirming its early presence in the lake and reinforcing evidence for slightly warmer glacial conditions.

A drier climate during HS5a-1 led to rapid lake level declines and affected both freshwater and terrestrial communities. Lower lake levels probably increased habitat availability for littoral ostracode species through expansion of aquatic plant cover (Cohuo et al., 2018). From 85.0 to 60.1 ka, representatives of Melastomataceae were the dominant taxa, and non-modern-analog vegetation was established. This suggests that climate and environmental conditions during that interval were different from those inferred for the rest of the glacial period.

Reduced precipitation with the onset of Heinrich stadials triggered rapid shifts from more mesic to dry forests. Climate conditions became drier as the stadials progressed, and there was a change from dry seasonal scrub to xeric shrubland. Vegetation surrounding Lake Petén Itzá displayed profound shifts during the stadials, but especially later, at the onset of the Holocene, when relative abundance of Moraceae increased dramatically, indicating warmer and wetter conditions (Correa-Metrio et al., 2012a, 2012b) (Figs. 2, 3).

Magnitude and velocity of ecological turnover of freshwater and terrestrial communities during HS6-1

DCA sample scores for ostracodes and pollen from the ~85-ka Petén Itzá record show that (1) the ostracode community was more dynamic than the surrounding vegetation (larger DCA scores), and (2) major changes in climate and environmental conditions of the northern neotropics occurred in the interval between about 62 and 51 ka, and at the Pleistocene/Holocene transition (Fig. 4a and b). The ostracode and pollen DCA values and *a priori* knowledge about ecological preferences suggest generally colder (Fig. 4b) and drier (higher E/P and conductivity, Fig. 4a) conditions during Heinrich stadials, except HS6 and HS5a. The interval from HS6 to HS5a (62.5–53.1 ka) was, instead, warmer and drier (DCA-adults axis 1). Our results also suggest slightly warmer conditions during the termination of HS2. Vegetation, on the other hand, clearly responded to increases in both temperature and precipitation at the Pleistocene/Holocene transition.

Traditionally, paleoecological studies use shifts in species composition and relative abundance to infer past climate and environmental changes. We, however, used DCA to quantify past ecological change (expressed as SD) and the velocity of change (SD/100 yr) of aquatic and terrestrial communities during the last ~85 ka in and around Lake Petén Itzá. The discovery that ostracode responses to changes in temperature and E/P were faster than vegetation responses is similar to findings at Lago Verde, Mexico, in which counts of diatoms and pollen were compared (Correa-Metrio et al., 2014a); aquatic bioindicators track environmental change more rapidly, probably because of their short life cycles.

Overall, the high and frequent ecological turnover in the Lake Petén Itzá record suggests that temporal patterns of diversity are similar to those that characterize modern geographic space; i.e., there is low alpha (local) and high beta (regional) diversity. Major and rapid aquatic and terrestrial ecological changes (Fig. 4c–f) coincided with abrupt climate and environmental shifts (Fig. 4a and b) in lowland Central America, which occurred during HS6-1 and at the Pleistocene/Holocene transition.

Although we were able to document ostracode and vegetation responses to warm/dry (HS6, HS5a) and cold/dry (HS5-1) conditions, taxa abundances, DCA sample scores, and magnitudes and rates of biotic change displayed differences among Heinrich stadials. Such differences are more pronounced in the ostracode record. For instance, large changes were observed at the onset and termination of HS5a, HS4, HS3, and HS1, whereas a large ecological change characterized only the onset of HS5, but later decreased. The ecological change during HS6 and HS2 increased relatively slowly. Our study shows that vegetation turnover during the past 85 ka was rather slow and progressive, whereas ostracode assemblages displayed relatively abrupt responses to climate and environmental changes.

Rates of ecological change were high during Heinrich stadials, and velocity increased from HS6 to HS1. HS1 was identified as the coldest and driest stadial (Cohuo et al., 2018), which may explain the high velocity of ecological change (Fig. 4e and f). The magnitude of ecological change during HS1, however, was lower than for other stadials (Fig. 4c and d). Ostracode and vegetation communities during HS6 and HS5 underwent both large and rapid species turnover. This highlights the fact that aquatic and terrestrial communities may respond to different extents and at different rates to climate change, with other factors such as life history of taxa, species interactions, and perhaps random drift influencing community responses.

Inferences about climate and environmental conditions at Lake Petén Itzá over the last 85 ka showed two intervals of major biological change and hence distinct climate and environmental conditions. Conditions during HS6 and HS5a were unexpectedly warm and dry, whereas after 53 ka, HS5-1 was cold and dry, and probably linked to climate and hydrological processes in the North Atlantic (Cohuo et al., 2018). Future studies, combining biotic and abiotic proxy climate data from Lake Petén Itzá and other lake and marine sediment records, and speleothems from the region, along with paleoclimate model simulations, should help explain the anomalous conditions of HS6 and HS5a in the northern neotropics. Such studies will also enable inferences about climate and environmental conditions at a broader spatiotemporal scale. This study shows the potential of the Lake Petén Itzá record to shed light on the differential modulation of the Atlantic and the Pacific Oceans on millennial-scale climate dynamics in Central America.

CONCLUSIONS

Environmental inferences based on ostracode and pollen in sediments from Lake Petén Itzá illustrate how lowland neotropical freshwater and terrestrial ecosystems were modified by abrupt climate change during HS6-1 and the subsequent transition from the Pleistocene into the Holocene in northern Central America. Repeated abrupt declines in the number of ostracode and vegetation taxa were discernible during HS5-1. In contrast, ostracode species richness and diversity were high during HS6 and HS5a. Our paleoecological study of aquatic and terrestrial bioindicators confirmed that conditions in the region were cold and dry during HS5-1, but revealed unexpected slightly warmer and dry conditions from HS6 to HS5a.

Ostracode communities were more dynamic and sensitive than terrestrial plant communities, displaying both larger-magnitude and more rapid responses to climate and environmental changes. Nevertheless, both freshwater and terrestrial records showed similar patterns of change that complemented one another, especially prior to 50 ka, when ostracode abundances were low. Ostracode responses usually preceded those of vegetation; i.e., the freshwater invertebrates responded more rapidly. Despite pronounced and sometimes rapid shifts in environmental conditions in Lake Petén Itzá, endemic ostracodes *P. opesta* and *C. petenensis* were sufficiently adaptable over the past 85 ka to persist in the modern ostracode community. Glacial vegetation was dominated mainly by *Quercus*, *Pinus*, and Cyperaceae. Transitions from mesic to dry forests were triggered by decreases in precipitation, and as climate dried during Heinrich stadials, seasonal scrub transitioned to xeric shrubland.

The interval from HS6 to HS5a in northern Guatemala displayed large biotic changes and unique glacial climate conditions (warm and dry), which we suspect were related to climate conditions in the Pacific and/or western Caribbean Sea. After 53 ka, however, the Petén Itzá record seems to track North Atlantic events. Both the ostracode and pollen records indicate a rapid and pronounced shift from cold and dry to warm and wet conditions at the Pleistocene/Holocene transition.

Acknowledgments. We thank all our colleagues and the institutions involved in the Petén Itzá Drilling Project. Special thanks to Flavio Anselmetti, Daniel Ariztegui, Kristina Brady, Mark Bush, Jaime Escobar, Andreas Mueller, Amy Myrbo, Anders Noren, David Hodell, Christine Paillès, Douglas Schnurrenberger, Florence Sylvestre, and the National Lacustrine Core Repository (LacCore, University of Minnesota). Susanne Krüger assisted with ostracode extraction and counting. Burkhard Scharf and Dietmar Keyser helped establish the ostracode taxonomy and prepare the SEM images for identification. We appreciate discussions with Florence Sylvestre, Christine Paillès, and Guillaume Leduc (Centre Européen de Recherche et D'Enseignement des Géosciences de L'Environnement). Matthias Bücker edited the bathymetric map. The Universidad del Valle de Guatemala and the Consejo Nacional de Áreas Protegidas assisted with import and export of scientific equipment and samples, and with securing scientific sampling permits.

Financial Support. Funding was provided by the Deutsche Forschungsgemeinschaft (DFG grants 5448462, 235297191, 252760755, 439719305), Technische Universität Braunschweig, Swiss Federal Institute of Technology, Swiss National Science Foundation, US National Science Foundation, and the International Continental Scientific Drilling Program. Schenk received funding from the Swedish Research Council (VR 2015-04418).

Data availability. Biological data (abundances, DCA scores, ecological change, and rates of ecological change) will be uploaded and available in PANGAEA.

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