INFLUENCE OF LATE QUATERNARY CLIMATE ON THE BIOGEOGRAPHY OF NEOTROPICAL AQUATIC SPECIES AS REFLECTED BY NON-MARINE OSTRACODES

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Abstract

We evaluated how ranges of four endemic and non-endemic aquatic ostracode species changed in response to long-term (glacial-interglacial cycles) and abrupt climate fluctuations during the last 155 ka in the northern Neotropical region. We employed two complementary approaches, fossil records and species distribution modeling (SDM). Fossil assemblages were obtained from sediment cores PI-1, PI-2, PI-6 and Petén-Itzá 22-VIII-99 from Petén Itzá Scientific Drilling Project, Lake Petén Itzá, Guatemala. To obtain a spatially resolved pattern of (past) species distribution, a downscaling cascade is employed. SDM's were reconstructed for the Last Interglacial (~120 ka BP), the Last Glacial Maximum (~22 ka BP) and the middle Holocene (~6 ka BP). During glacial/interglacial cycles and Marine Isotope Stages, modeled paleo-distributions and paleo-records show nearly continuous presence of endemic and non-endemic species in the region, suggesting negligible effects of long-term climate variations on aquatic niche stability. During periods of abrupt ecological disruption such as Heinrich Stadial 1 (HS1), endemic species were resilient, remaining within their current areas of distribution. Non-endemic species, however, proved to be more sensitive. Modeled paleo-distributions suggest that the geographic range of non-endemic species changed, moving southward into Central America. Due to the uncertainties involved in the downscaling from the global numerical to the highly

resolved regional geospatial statistical modelling, results can be seen as benchmark for future studies using similar approaches. Given relatively moderate temperature decreases in Lake Petén Itzá waters (~5ºC) and persistence of some aquatic ecosystems even during periods of severe drying in HS1, our data suggest 1) existence of micro-refugia and/or 2) continuous interaction between central metapopulations and surrounding populations, enabling aquatic taxa to survive climate fluctuations in the northern Neotropical region.

Keywords: Climate change, freshwater ostracodes, Neotropics, fossil records, species niche modelling.

1 Introduction

Climate changes are quasi-cyclical natural processes that continuously influence ecosystem dynamics and shape biological diversity worldwide (Blois et al,. 2013; Parmesan and Yohe, 2003; Yasuhara et al., 2009; 2017). On inland ecosystems Late Quaternary climate fluctuations such as glacial/Interglacial cycles are recognized as the main drivers responsible for past species extinctions (Martínez-Meyer et al., 2004; Nogués-Bravo et al., 2008), speciation events (Peterson and Nyári, 2008; Solomon et al., 2008), delimitation of refugia (Hugall et al., 2002; Peterson et al., 2004) and development of migration pathways (Ruegg et al., 2006; Waltari and Guralnick, 2009) for both plants and animals.

In the northern Neotropics, which include southern Mexico, Central America and the Antilles, late Quaternary climate inferences based on climatic simulations with global climate models (GCMs) (Hijmans et al., 2005) and reconstructions from marine and lacustrine sedimentary sequences (Hodell et al., 2008; Pérez et al., 2011, 2013; Escobar et al., 2012) have revealed climate fluctuations related to temperature and precipitation, especially during transitions between glacial and interglacial episodes, and during climate pulses such as the Last Glacial Maximum (LGM) and Heinrich stadials (HS) (Correa-Metrio et al., 2012b). In the Neotropics, controls of climate fluctuations are related to orbital forcing and internal component variations, such as the position (north-south) of the inter tropical convergence zone (ITCZ), strength of Atlantic meridional overturning circulation (AMOC) and changes in Caribbean surface

water temperature (Cohuo et al., 2018). Alterations in these features have produced temperature decreases in a range of 3 -5⁰C, although some estimations suggest decreases up to 10⁰C relative to present and large reductions in precipitation, particularly during HS, when most lakes in the region dried completely (Cohuo et al., 2018). Correa-Metrio et al. (2014) found evidence for rapid climate change in terrestrial environments during HS, which was associated with major ecological and biological shifts (Loarie et al., 2009; Burrows et al., 2011; Sandel et al., 2011). Correa-Metrio et al. (2012a, b,2014) found that plant survival in the northern Neotropical region during HS required migrations to refugia. The climatically driven pace and magnitude of changes in aquatic environments can, however, vary considerably relative to effects in terrestrial environments (Sandel et al., 2011; Litsios et al., 2012; Bonetti and Wiens, 2014). It therefore remains uncertain how aquatic species responded to past climate alterations.

To evaluate past biogeographic dynamics of northern Neotropical inland aquatic species, we used freshwater ostracodes (bivalved microcrustaceans) as a model group (Mesquita-Joanes et al., 2012), and two complementary approaches (1) fossil records (Dawson et al., 2011; McGuire and Davis, 2013) and (2) species distribution models (SDM) (Elith and Leathwick, 2009; Nogués-Bravo et al., 2009; Veloz et al., 2012; Maguire et al., 2015).

Ostracodes were selected because they possess one of the best fossil records in the region since the Late Quaternary (Pérez et al., 2011, 2013) and have demonstrated to be sensitive to climatic variation (at modern and past) in both terrestrial (Horne et al., 2002) and marine environments (Yasuhara et al., 2008, 2014). Given their intermediate role on trophic chains (Valtierra-Vega and Schmitter-Soto, 2000; Bergmann and Motta, 2005; Cohuo et al., 2016), changes in their abundances and assemblage composition can also reflect changes in primary production and higher trophic levels (Rodriguez-Lazaro and Ruiz-Muñoz, 2012). Paleorecords provide true evidences for the presence of a species within the past, at resolutions ranging from decadal to millennial scales, but in absence of a denser spatial network, this approach is usually limited to the local scale (Maguire and Stigall, 2009; Dawson et al., 2011). Species distribution models are based on the combination of georeferenced species occurrences with environmental information to characterize the range of climate tolerance that a species inhabits (Guisan and Thuiller, 2005;

Maguire et al., 2015). By using multiple time periods, species occurrences across different climatic scenarios can be projected to a certain degree (Elith and Leathwick, 2009; Svenning et al., 2011).

Most important limitations and uncertainties of SDMs are the according forcing data such as GCMs and the statistical algorithms employed. For instance, simulations of tropical Atlantic climates remain deficient in many climate models due to incomplete characterization of the vertical structure of tropospheric water vapor and humidity. As a consequence, the simulation of temperature and precipitation gradients is afflicted with a high degree of uncertainty in GCM's, especially across regions with irregular and complex topography (Solomon et al., 2010). Statistical algorithms and data parametrization also add another level of uncertainty in the downscaling cascade, including the structure of past surface fields such as topography, vegetation structure and coastline. Moreover, the usage of statistical algorithms for the geospatial mapping also includes uncertainties that are implicitly included in the results (Chen et al., 2010; Neelin et al., 2010).

The combination of paleorecords and SDM's, provides a unique opportunity to obtain quantitatively and potentially high-resolution reconstructions of past species dynamics at local and regional scale during past climate fluctuations in the northern Neotropical region.

In this study, we addressed three overarching questions: 1) Did past climate changes since 155 ka BP (Hodell et al., 2008; Correa-Metrio et al., 2012a, b, 2014; Cohuo et al., 2018) have profound consequences for aquatic ecosystem stability in the northern Neotropics? 2) Did endemic and non-endemic (widespread) species respond in the same way to climate shifts? 3) Did refugia exist, and if so, what was their spatial distribution?

2 Methods

2.1 Study area and sampling of modern species

Our study area is the northernmost northern Neotropics, an area that extends from southern Mexico to Nicaragua (Fig.1). We sampled 205 aquatic ecosystems during 2010–2013, including *cenotes* (sinkholes), lakes, lagoons, crater lakes, maars, permanent and ephemeral ponds, wetlands, and flooded caves. Sampled systems are located at elevations from ~10 to ~4000 m a.s.l., and conductivity ranged from

4

137   0.1 to 3500 µS cm^{-1}. Most aquatic systems were shallow with a mean depth < 10m,

138   except for large lakes such as Petén Itzá, Atitlán, Coatepeque, Ilopango, Lachuá,

139   crater and maar lakes and cenotes which are mostly >15m deep. Biological samples

140   were collected at three different sections of the systems; littoral, water column and

141   deepest bottom. At littoral areas, we sampled in between submerged vegetation

142   using a hand net of 250 µm open mesh. Water column was sampled doing vertical

143   tows and horizontal trawls with a net of 20 cm-wide mouth and 150 µm mesh size.

144   Sediment samples were taken from the deepest part of the systems with an Ekman

145   grab, but only the uppermost centimeters of each grab were used for further analysis.

146   Ostracodes were sorted in the laboratory using a Leica Z4 stereomicroscope and

147   dissections were carried out in 3% glycerin. Shells were mounted on

148   micropaleontological slides. Dissected appendages were mounted in Hydromatrix®

149   mounting media. Taxonomic identification followed Karanovic, (2012) and Cohuo et

150   al. (2016). Four ostracode species were selected for this study: *Cypria petenensis*

151   Ferguson et al., 1964, *Paracythereis opesta* (Brehm, 1939), representing taxa

152   endemic to the northern Neotropical region (Cohuo et al., 2016) (Fig. 1A, B), and

153   *Cytheridella ilosvayi* Daday, 1905 and *Darwinula stevensoni* (Brady & Robertson,

154   1870), which are widely distributed (non-endemic) on the American continent (Fig.

155   1C, D).

156   **2.2 Sediment cores from Lake Petén Itzá and regional paleo-records**
157

158   Information about fossil occurrences of the target species was obtained from

159   sediment cores retrieved from Lake Petén Itzá (northern Guatemala), by the Petén

160   Itzá Scientific Drilling Project (PISDP). Cores PI-1, PI-2, PI-6 (Mueller et al., 2010)

161   and Petén-Itzá 22-VIII-99 were used. Core chronologies were established

162   independently by radiocarbon dating (Mueller et al., 2010) and for cores PI-1, PI-2,

163   PI-6, sediments older than 40 ka were dated by identification and correlation of

164   tephra layers (tephrochronology) (Kutterolf et al., 2016). The age model proposed by

165   Kutterolf et al. (2016) was used. Correlation of cores was done using lithological

166   markers, stratigraphic boundaries, similarity in magnetic susceptibility patterns and

167   ash layers correlation such as Congo tephra, 53 kyr BP, EFT tephra, 50 kyr BP and

168   Mixta tephra ~39 kyr BP. Core Sampling was done at 20 cm intervals, which is ~100 -

169   200 yrs of temporal resolution (Kutterolf et al., 2016). At sediment transitions and

170 periods of interest such as LGM and Heinrich Stadials, samples were closely spaced

171 at 1 cm, representing ~ 6 - 10 yrs of temporal resolution (Kutterolf et al., 2016). All

172 samples had a volume of 3 cc of wet sediments.

173

174 Ostracode separation methods and counting can be found Cohuo et al. (2018). We

175 looked at near-continuous ostracode fossil occurrences in the sediments over the last

176 155 ka. There was, however, a gap in sediments availability during the period 83-53

177 ka BP. We also compiled fossil data for our target species from 19 other studies in

178 the northern Neotropical region, to obtain past spatial distributions of the target

179 species (Supplementary material, Table S1). These studies were restricted to the

180 LGM and middle Holocene.

181 Shells of the target species were measured and photographed using a Canon

182 Powershot A640 digital camera attached to a Zeiss Axiostar-plus light microscope.

183 Abundances of the target species in each core were plotted using C2 software

184 version 1.5 (Juggins, 2007).

185 **2.3 Species niche modelling (SNM): modern projections and reconstruction of**

186 **past distributions**

187 We determined modern macro- and micro-ecological preferences for our target

188 species using our data set (multivariate approach) and the literature (Pérez et al.,

189 2010). Given the ecological preferences of the species, we used seven environmental

190 variables related to temperature and precipitation that show the lower Pearson

191 correlation coefficient within 19 regional environmental variables (Supplementary

192 material, Table S2), and are known to have the strongest relationships with ostracode

193 distribution: 1) mean annual temperature, 2) mean diurnal temperature range, 3)

194 isothermality (day-to-night temperature oscillation relative to summer-to-winter), 4)

195 temperature seasonality, 5) annual temperature range, 6) total annual precipitation,

196 and 7) precipitation seasonality, all available from the WorldClim database version 1.4

197 (Hijmans et al., 2005; http://www.worldclim.org). Variables of importance were

198 analyzed to identify those with greatest influence on each ostracode species

199 distribution.

200 Environmental conditions of the present corresponded to the interpolation of average

201 monthly climate data from weather stations of various locations of the world and major

climate databases such as the Global Historical Climatology Network (GHCN) and the Food and Agricultural Organization of the United Nations (FAO). Grids had a spatial resolution of 30-arc second. Although modern climatic data is generated at very high resolution, one should note that modelling of tropical climate and circulation is still afflicted by a comparatively high degree of uncertainty, especially the realistic simulation of the hydrological cycle and precipitation. In this context, the purpose of the study is also to investigate how far differences in profound background climatic changes during Glacial-Interglacial periods are responsible for lateral and/or vertical changes in ecological niches of the respective species.

Past species distributions were investigated using climate conditions inferred for three time periods: ~120 ka BP (last interglacial), ~22 ka BP (Last Glacial Maximum [LGM]) and ~6 ka BP (middle Holocene). For environmental data corresponding to ~120 ka BP (Otto-Bliesner et al., 2006), grids have a spatial resolution of 30-arc seconds, which represents ~1 km^2 in the northern Neotropical region. Environmental conditions at ~22 and ~6 ka BP were obtained from downscaled paleoclimatic simulations forced with the coarsely resolved output fields of two global circulation models (GCMs), the MIROC-ESM 2010 (Watanabe et al., 2011) and CCSM4 (Gent et al., 2011).
These GCMs were selected because they yield slightly varying temperature and differences in precipitation fields (Fig. 2). At ~22 ka BP, the MIROC-ESM model shows colder and drier conditions in the region than does the CCSM4 model (Fig. 2). At ~6 ka BP, the CCSM4 model simulates slightly cooler and drier conditions than does the MIROC-ESM model (Fig. 2). These differences enable assessment of model uncertainty with respect to global climate simulations.

The target grids at the lower end of the downscaling cascade have a spatial resolution of 2.5-arc minutes, which represents ~5 km^2 in the study area. For all periods, grids with global information were trimmed to match the extent of our study area. The SDM toolbox (Brown, 2014), implemented in Arc GIS, was used for this purpose.

The modeling framework was constructed using five presence/absence-based algorithms because of true species absences in our database. We used the Generalized Linear Model (GLM) (McCullagh and Nelder, 1989), the Generalized Additive Model (GAM) (Hastie and Tibshirani, 1990), the Generalized Boosting Model (GBM) (Ridgeway, 1999), Maximum Entropy (MAXENT) (Tsuruoka, 2006) and the

Surface Range Envelope (SRE) (Busby, 1991). The first three algorithms, GLM, GAM and GBM are regression-based models, which are flexible to handle a variety of data responses types (linear and non-linear) and are less susceptible to overfitting than other algorithms such as multivariate adaptive regression splines (MARS) (Guisan et al., 2002; Franklin, 2010). MAXENT is a general-purpose machine learning method which predicts a species probability occurrence by finding the distribution closest to uniformity (maximum entropy), it requires previous knowledge of the environmental conditions at known occurrence localities (Elith et al., 2011). The SRE algorithm is an envelope-type method that uses the environmental conditions of locations of occurrence data to profile the environments where a species can be found (Araujo and Peterson 2012). All these modelling techniques are at different degree limited by several numerical factors, such as missing values, outliers, sampling size, overfitting and interaction between predictors. Special attention therefore must be paid to produce reliable models which maximizes the agreement of the predicted species occurrences with the observed data (Guisan et al., 2002; Franklin, 2010). In most cases the combination of methods (e.g. GLM and GAM) is recommended to assess the robustness of according results of individual models (Guisan et al., 2002).

For our study, settings for all modeled techniques, such as the number of trees, number of permutations, iteration depths, Bernoulli distribution normalization and node-size, follow George and Thuiller (2013). Records were split randomly into a training (calibration) (70%) and a test (validation) (30%) dataset, with 10 replications for each model type. A total of 50 models (5 algorithms and 10 replications) were generated for each ostracode species and time period. All projections were evaluated using three statistical approaches, to reduce uncertainty in species niche models: 1) The true skill statistics (TSS), (2) the area under the receiver operating characteristic curve (AUC) and (3) Cohen's Kappa statistics (Thuiller et al., 2009, 2015). For all algorithms, best-fit model runs above critical values (TSS values >0.4, AUC >0.7 and KAPPA >0.4) were used to construct consensus maps for each modeling technique. Final maps were constructed using an ensemble of all techniques. The combination of methods reduces the effect of inter-model variability and uncertainties that arise from using single algorithms (Araújo and New, 2007; Marmion et al., 2009; Thuiller et al., 2009). The final distribution maps thus indicate areas simulated by most modeling techniques. All calculations were done using the 'biomod2' v.3.1-64 package (Thuiller et al., 2015), implemented in R v.3.2.1 software (R Development Core Team, 2015).

3 Results

3.1 Northern Neotropical paleorecords, species permanence and displacement

Records of the period corresponding to the Last Interglacial (130-115 ka BP), were obtained from core PI-7 (155-83 ka BP). Abundances of our four target species were generally low, with <60 adult shells gr^{-1}, and frequencies (relative abundances) varied considerably (Fig. 3). The endemic *C. petenensis* was the most frequent species (Fig. 3). *Paracythereis opesta* and *C. ilosvayi,* which are bottom-dwelling organisms, were recovered only from sediments deposited ca. 87-85 ka BP, where high abundances of *C. petenensis* were observed (Fig. 3). *Darwinula stevensoni* showed a sole occurrence at ~155-153 ka BP.

Records of the Last Glacial and Deglacial were obtained from Lake Petén Itzá core PI-2 (Fig. 4A) and published data from core PI-6 (Fig. 4B) (Pérez et al., 2011). Pérez et al. (2011) found nearly continuous presence of endemic species in core PI-6 during the interval 24-10 ka BP. Gaps of millennial duration are, however, evident for the periods 24–22 and 13–10.5 ka BP. The record from PI-2 shows a complementary pattern to that of PI-6, because species presence in PI-2 coincided with species absence in core PI-6. *Cypria petenensis* in the PI-2 record, for example, shows high abundances at the onset of the LGM (23-21 ka BP), and *P. opesta* displays high abundances around 22 and 19 ka BP (Fig. 4A). Thus, the two records suggest continuous presence of endemic species in Lake Petén Itzá during both the LGM and Deglacial.

Non-endemic species show intermittent distributions in both the PI-2 and PI-6 cores (Fig. 4A, B). *Darwinula stevensoni* was recorded exclusively at ca. 23, 22-20, and 19-18 ka BP, the latter at the onset of the Deglacial. Similarly, *Cytheridella ilosvayi* was present in very low abundances during two short episodes at about 20 and 14 ka BP. We recorded low abundances of both species during the LGM (<250 adult shells g^{-1}), compared to periods immediately before and after, when temperatures are thought to have been warmer. For example, during the Deglacial, abundances were always >250 adult shells g^{-1}.

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Fossil records from the middle Holocene were obtained from core Petén-Itzá 22-VIII-99 and eleven regional studies (Fig. 5A). The record from core Petén-Itzá 22-VIII-99, retrieved from 11.5 m water depth, shows that endemic species were present continuously during the last 6.5 ka (Fig. 5A). Most regional records came from *cenotes* and lakes on the Yucatán Peninsula (Supplementary material, Table S1). All fossil records show that endemic species were spatially distributed throughout the current ranges of extant populations (Fig. 5B).

For non-endemic species, regional fossil records from the middle Holocene revealed their presence ranging from the northern Yucatán Peninsula to northern Guatemala and Belize (Supplementary material, Table S1). Core Petén-Itzá 22-VIII-99 highlights an almost continuous presence of *C. ilosvayi* in the lake, characterized by high abundances, except for the period 11-8.5 ka BP, when the species was absent (Fig. 5A). *Darwinula stevensoni* was present continuously during the last 9 ka, but in the lower section of the core, dated to 14-10 ka BP, the species was absent (Fig. 5A).

3.2 Species niche modeling: distribution hindcasting for time slices ~120, ~22 and ~6 ka BP

For the 205 aquatic ecosystems sampled, 145 had at least one of the target species present: *C. petenensis, P. opesta, C. ilosvayi* and *D. stevensoni*. Forty-nine systems contained *C. petenensis*, 37 had *P. opesta*, 79 were inhabited by *C. ilosvayi*, and 61 contained *D. stevensoni*. Analysis of variables of importance showed that environmental variables with the greatest influence on species distribution are precipitation seasonality and mean annual temperature (Table 1). For individual species, however, variables received different scores, indicating that each species optimal climate niche is controlled by a particular combination of variables (Table 1). Diagnostic tests of the reconstructions (TSS, AUC and Kappa) show good performance for all algorithms and periods evaluated (Table 1). There were, however, differences in predictive accuracy within species. Modeled distributions of endemic species have the highest evaluation scores (AUC =0.8, TSS=0.49, Kappa=0.45). Non-endemic species models (AUC=0.75, TSS=0.46, Kappa=0.46) have slightly lower values, but also fall within the acceptable range.

Reconstructions for the period ~120 ka BP suggest very broad distributions of endemic taxa, as climate enabled the species to expand their ranges. Probability values, however, were relatively low (<80%) (Fig. 3B). For the non-endemic species,

reconstructions for ~120 ka BP show different areas of climatic suitability, with species presence probabilities reaching 60%. Zones of higher probability (>80%) are dispersed throughout the region. The most extensive zones of species distribution suitability are located along the Caribbean coast of the Yucatán Peninsula and in northern Guatemala (Fig. 3B).

Inferences for endemic taxa distributions at ~22 ka BP, based on the CCSM4 model, suggest that these species remained in the core area, but that they may have been displaced somewhat to the northern portion of the Yucatán Peninsula (Fig. 4C). This estimate has probability values of >75%. The MIROC-ESM model suggests areas of distribution similar to those presented by the CCSM4 model, but slightly more restricted areas for *C. petenensis* and more widespread areas for *P. opesta.* Probability values were low in this model (<65%) (Supplementary material, Fig. S1). Models for non-endemic species reveal fragmented and discontinuous distributions (Fig. 4C). At ~22 ka BP, corresponding to the LGM, both the CCSM4 and MIROC-ESM models suggest that non-endemics moved northward on the Yucatán Peninsula to the Gulf of Mexico (>65% probability), and/or were displaced southward to Central America (85% probability) (Fig. 4C; Supplementary material, Fig. S1).

For ~6 ka BP, the CCSM4 model suggests discontinuous areas of distribution on the Yucatán Peninsula (Fig. 5B) for endemic species, whereas the MIROC-ESM shows more continuous distributions, particularly along the eastern portion of the Peninsula (Supplementary material, Fig. S1). For non-endemic species, the CCSM4 and MIROC-ESM models show very similar patterns. Extensive regions of climatic suitability were identified for *C. ilosvayi*, but those with higher probability are located along the Caribbean Coast (Fig. 5B; Supplementary material, Fig S1). For *D. stevensoni*, areas of maximum probability are discontinuous. Maximum probability was found at isolated regions such as the southern part of the northern Yucatán Peninsula, Belize and eastern Honduras (Fig. 5B).

4 Discussion

4.1 Congruence between paleo-records and modeled paleo-distributions of freshwater ostracodes in the northern Neotropical region

Our study highlights the fact that accuracy and congruence between paleo-records and modeled paleo-distributions of freshwater ostracodes in the northern Neotropical region was influenced by multiple factors such as climate model used, modeling algorithm employed, sediment core characteristics and target species.

For instance, distribution models and modelling cascade were characterized by high degree of uncertainty with regard of precipitation and temperature estimations of climate models (GCMs). This limited the full estimation of spatial distribution of target species, especially during older periods such as LIG and LGM were fossil evidence (spatial and temporal) was scarce.

The simulation of precipitation of GCMs is afflicted with high degrees of uncertainties, because the vertical structure of stratospheric water vapor and humidity profile have large biases, especially in the tropics (Gettelman et al., 2010). This implies that GCMs commonly reproduce large-scale pattern of precipitation with high confidence but models tend to underestimate the magnitude of precipitation change at regional or local scale (Stephens et al., 2010). Similarly, GCMs temperature estimations in the tropics may display large biases, because changes in climate drivers of continental temperature of the northern Neotropics such as Atlantic sea surface temperature and the Atlantic warm pool, are usually underestimated (Liu et al., 2013). Simulations of temperature variations during LGM, for example, tend to overestimate cooling in tropical regions (Kageyama et al., 2006; Otto-Bliesner et al., 2009).

In our study, reconstructed maps based on MIROC-ESM and CCSM4 models, simulate slightly different areas of distribution for the target species. This is associated to differences in precipitation and temperature estimations between models. The most important difference between their respective reconstructions pertains to the extent of suitable areas of distribution of the species, being generally broader in MIROC-ESM model than in CCSM4 model.

The scarcity of fossil records also limited the full reconstruction of distribution dynamics of species, especially during LIG and LGM, because records were obtained only from Lake Petén Itzá and were relatively scarce. The period 24-14 ka BP, was highly informative, because the comparisons between cores PI-2 and PI-6, and

specifically, the compensation effect between them (the presence of species in a core in periods were absences were determined in the other), highlight that gaps in the fossil record may be related to core location in the lake, shell preservation and individual species ecology and not only by species absence. This therefore, suggest that short gaps, lasting less than 10 ka cannot be considered evidence for species absence.

In general, the comparison between species distribution models and paleorecords shows a quite high degree of similarity. This is especially evident for the middle Holocene as the individual SMD output of the target species were compared with the fossil records at regional scale. In all cases, SDMs reconstructions shows distributional areas where fossil records were recovered. This congruence may be supported by the agreement between estimations of temperature in climate models and paleorecords.

4.2 Endemic and non-endemic species responses during long-term climatic fluctuations: Glacial/Interglacial cycles and Marine Isotope Stages

Paleoclimate inferences derived from Lake Petén Itzá sediments suggest that Glacial/Interglacial cycles in the northern Neotropical region did not have profound consequences with respect to the spatial distribution of isotherms in terrestrial environments (Hodell et al., 2008; Pérez et al., 2011; Escobar et al., 2012; Pérez et al., 2013). Most paleoclimate studies in the region based in different proxies such as ostracods, pollen, and $\delta^{18}O$ fluid inclusion data from speleothems suggest that temperatures during the last glacial and start of the deglacial may have been up to 5^0C lower than today (Correa-Metrio et al., 2012a, b; Arienzo et al., 2015; Cohuo et al., 2018), although some estimations suggest a temperature depression of about 10^0C compared with modern records (Hodell et al., 2012; Grauel et al., 2016). Precipitation was affected more profoundly, but not consistently during glacial-interglacial cycles and likely fluctuated in response to changes in local atmospheric circulation. For instance, the position of the Hadley cell and ITCZ, together with climate forcing, such as Heinrich Stadials, seem to drive precipitation fluctuation locally. During the LGM, for example, humid conditions has been estimated to the region (Cohuo et al., 2018).

428 Our results, however, suggest that temperature fluctuations affected aquatic species
429 associations to a higher degree compared to reductions in precipitation (changes in
430 lake water chemistry), because presence/absence of species and fluctuations in total
431 abundances match periods of temperature change, rather than times of lake level
432 shifts.

433 Endemic and non-endemic species responded similarly to Glacial and Interglacial
434 cycles and transitions. Fossil records from Lake Petén Itzá sediment cores PI-1, PI-2,
435 PI-6, and Petén-Itzá 22-VIII-99 reveal that endemic species were almost continuously
436 present during the last 155 ka. Short gaps, lasting less than 10ka were not considered
437 evidence for species absence.

438 Non-endemic species show patterns of expansion and contraction that track
439 temperature fluctuations. Modeled paleo-distributions and paleo-records show that
440 distributions of non-endemic species were widespread during the LIG and
441 fragmented during the middle Holocene, when climates were warmer. During the Last
442 Glacial, non-endemic species were absent or sporadically present. This may result in
443 response to lower temperatures characterized the LG. Modeled paleo-distributions
444 for the LGM also show that non-endemic species were displaced from their current
445 ranges toward the northern Yucatán Peninsula and/or southward toward Central
446 America, where a warm climate likely persisted. This scenario suggests migrations of
447 regional magnitude, as species were lost from areas such as southern Mexico and
448 northern Guatemala but persisted within their current range of distribution in
449 fragmented populations, such as areas of southeast Honduras and northeast
450 Nicaragua.

451 The presence of endemics and absence of non-endemic species during the LGM,
452 reveal a clear ecological signal, which may be associated to the degree of adaptation
453 to ecological niches. Endemic species seem to be highly resilient to long-term natural
454 disturbances, whereas non-endemic demonstrated to be more sensitive. There is
455 increasing evidence that biological communities, particularly terrestrial taxa, display
456 strong resilience in the face of natural and human disturbances in the northern
457 Neotropical region. Hurricane impacts, widespread pre-Columbian agricultural
458 activities, and decadal-to-centennial climate changes are recognized as main
459 disrupters of Holocene ecosystem composition and function in the region. Such
460 perturbations, however, did not severely and permanently alter plant associations

461   such as moist forests (Bush and Colinvaux ,1994; Cole et al., 2014) and dry tropical

462   forests (Van Bloem et al., 2006; Holm 2017), which persisted in the region despite

463   these disturbances. Plant taxa of Panama demonstrated a recovery time of just

464   350yrs after strong deforestation by pre-Columbian agriculture (Bush and Colinvaux,

465   1994). Similarly, the rain forest in Guatemala recovered from Mayan alterations in a

466   time span of 80-260yrs (Mueller et al., 2010). Bird composition have also

467   demonstrated rapid recovery time after hurricane impacts, species compositions

468   affected in Central America and the Caribbean return to pre-hurricane conditions in

469   time periods ranging from months to years (Will, 1991, Wunderle et al., 1992;

470   Johnson and Winker, 2010).

471   The continuous presence of both endemic and non-endemic (except during the LGM)

472   ostracode species in the northern Neotropics during Glacial/Interglacial cycles, also

473   reflects the fact that aquatic ecosystem functionality was little altered during the last

474   155 ka. High abundance of ostracodes, which belong to intermediate trophic levels,

475   suggests high rates of primary production and ample food sources for higher

476   consumers, especially during the LIG and middle Holocene. During the LGM, the

477   presence of endemics and absence of non-endemics, along with lower total

478   ostracode abundances, suggest moderate alteration of aquatic ecosystem dynamics.

479   Reduced primary production and loss of poorly adapted species might also be

480   inferred for this period.

481   Marine Isotope Stages (MISs), which describe shorter periods of climate variability

482   than Glacial/Interglacial cycles, were also used to evaluate the distribution dynamics

483   of aquatic species. During MISs, ostracode composition remained relatively constant,

484   even across MIS boundaries (Fig. 6). Sediments from Lake Petén Itzá that correspond

485   to warmer periods MIS3 (57-29 ka BP) and MIS1 (14 ka BP to present) were

486   characterized by abundant fossils. MIS2 (29-14 ka BP) shows lower species

487   abundances (total adult and juvenile valves), likely related to persistent cold

488   temperatures. The absence of *Cytheridella ilosvayi* during most of MIS2 illustrates the

489   sensitivity of non-endemics to cool temperatures (Fig. 6). Similar to

490   Glacial/Interglacials in terrestrial environments, during MISs, northern Neotropical

491   endemic species showed high resilience to changes between cold and warm phases,

492   whereas non-endemic species proved to be more sensitive to cold periods, especially

493   the LGM.

4.3 Species responses during abrupt climate shifts, and refugia for aquatic taxa

Sedimentological and fossil records from Lake Petén Itzá suggest that the periods of strongest climatic fluctuations during the last 155 ka BP in the northern Neotropics occurred around 85 ka BP (Mueller et al., 2010) and Heinrich Stadials (Correa-Metrio et al., 2012b; Cohuo et al., 2018). Those episodes were characterized by dramatic decreases in lake level, suggesting intense aridity in the region. Lowest estimated temperatures for the entire record correspond to HS1.

Correa-Metrio et al. (2013) estimated high climate change velocity in the region during HS1, which produced large changes in terrestrial plant communities. Correa-Metrio et al. (2012b, 2014) estimated that one of the consequences of such ecological instability was the substantial migration of tropical vegetation and development of refugia. The high velocity of climate change inferred for the northern Neotropical region is, however, opposite to trends observed elsewhere in the tropics, which suggest that high biodiversity and endemicity are associated with low climate change velocities and high species resilience (Sandel et al., 2011). It remains uncertain how climate change velocity during period of abrupt climate change affected aquatic communities in the northern Neotropical region. It is also unclear whether aquatic taxa were as dramatically affected as local terrestrial species during these abrupt episodes, or if they simply displayed high resilience.

We used the fossil record of freshwater ostracodes from HS's published in Cohuo et al. (2018) to analyze the HS1 structure in detail (Fig. 7), because that was the period of coldest temperatures and extreme drought during the last 85 ka (Mueller et al., 2010; Correa-Metrio et al., 2012a; Cohuo et al., 2018).

Estimated paleo-temperatures based on $\delta^{18}O$ fluid inclusion data and biological-based (ostracodes and pollen) transfer functions suggest an overall temperature decrease of about 5ºC in comparison with today temperatures during the HS1. With respect to temperature,environmental conditions probably remained suitable for tropical species (especially endemics) distribution across large areas of the Yucatán Peninsula and in northern Central America. Mueller et al. (2010) estimated that Lake Petén Itzá water level decreased by ~50 m during HS1, which would imply that lakes in the region with maximum depths <50 m, dried completely.

525 We assume that lakes that held water during HS1 served as "refugia" for aquatic taxa,
526 as temperature apparently did not limit species distributions (Cohuo et al., 2018).

527 Systems such as *cenotes* and lakes that are not directly dependent on precipitation to
528 maintain water level, but are instead controlled by large subterranean aquifers (Perry
529 et al., 2002; Schmitter-Soto et al., 2002; Vázquez-Domínguez and Arita, 2010) may
530 serve as "refugia" for aquatic species, enabling native species to remain in the region
531 during periods of low rainfall. To date, it remains uncertain whether lakes and *cenotes*
532 (approximately 7,000 in the Yucatán Peninsula) held water during HS1, and little is
533 known about their spatial distribution. Isolated water bodies (refugia) may explain the
534 high percentage of endemicity and micro-endemicity (species distributed in a single or
535 limited group of lakes) for aquatic taxa on the northern Yucatán Peninsula (Mercado-
536 Salas et al., 2013). Species that inhabited such systems may have remained isolated
537 and adapted to specialized environmental niches.

538 Deevey et al. (1983) studied sediment cores from Lakes Salpetén (z_{max} = ~30 m) and
539 Quexil (z_{max} = ~30 m), Guatemala, and inferred that most lakes, including *cenotes,* in
540 the northern Neotropics dried out during the Deglacial because of the hydrological
541 sensitivity of the region. They also found that most lake sediment cores from the
542 region bottom out at ~8 ka BP, which means that the lakes probably first filled in the
543 early Holocene, in response to wetter conditions and rising sea level, which raised the
544 local water table. The authors therefore suggested that only large lakes in the region,
545 with maximum depths >50 m (e.g. Petén Itzá, Macanché, Atitlán, Coatepeque,
546 Ilopango) held water during the dry Deglacial, but possessed water chemistry much
547 different from today, which limited habitats for aquatic species.

548 This second scenario favors the hypothesis of central populations (meta-populations)
549 in one or more large lakes, which enabled species exchange with surrounding aquatic
550 environments, thereby preventing species losses in small populations by demographic
551 stochasticity. The two scenarios are not mutually exclusive, and it is possible that both
552 account for the success of aquatic tropical taxa through periods of abrupt or prolonged
553 climate fluctuations. Lake Petén Itzá may have played an important role for aquatic
554 species survival and dispersal in the northern Neotropical region, because it held
555 water for at least the last 400 ka (Kutterolf et al., 2016).

556 Our findings contrast with results from terrestrial environments, which show that HS1

557 drove plant species to migrate and retreat to a few well-defined micro-refugia (Cavers

558 et al., 2003; Dick et al., 2003; Correa-Metrio et al., 2013). Burrows et al. (2011)

559 demonstrated that the pace of climate shifts in aquatic and terrestrial systems can be

560 very different. They estimated that vegetation responds rapidly to climate change,

561 especially to precipitation and temperature shifts. Indeed, changes in these variables

562 can alter the composition of vegetation abruptly, within a few years. Conversely, in

563 aquatic environments, the velocity of climate change tends to be slower. For instance,

564 given the geomorphology of water systems in the region such as cenotes (small area

565 <1km^2, and deep waters >10m) and large lakes as Petén Itzá (>120m deep), dramatic

566 changes in air temperatures are needed to alter the temperature of the water column

567 and thus impact species niche stability. Our study suggests that the velocity of change

568 in aquatic environments remained low in the northern Neotropical region, enabling

569 local species to adapt and specialize to their environments instead of migrating and/or

570 remaining isolated in refugia, as observed in tropical areas elsewhere.

571 **5 Conclusion**

572 Our study integrates species distribution models and paleorecords to reconstruct

573 aquatic species distribution dynamics during the last 155 ka BP in the northern

574 Neotropics. Both approaches show strengths and limitations. Species distribution

575 models were afflicted by a degree of uncertainty due to uncertainties of general

576 circulation models MIROC-ESM and CCSM4 simulations related to precipitation and

577 temperature. Although these uncertainties can be considered as systematic errors, it

578 remains uncertain whether the lower-end simulations based on SDMs generated in

579 this study, fully reconstruct suitable areas of distribution of aquatic species, especially

580 because in tropical regions the larger biases on simulated values of precipitation and

581 temperature have been estimated.

582 Most important limitations of paleorecords relate to the scarcity of fossil evidence

583 spatially and temporally, especially for the older periods evaluated. Low abundances

584 in ostracodes were associated to species ecological preferences, core location and

585 preservation processes. The integration of fossil evidence from two long cores of the

586 Lake Petén Itzá was highly informative as the full range of temporal

587 presence/absence of the target species were recovered.

In spite, limitations of both approaches, the comparison of SDM outputs and fossil records, resulted in congruent patterns. For the older periods such as LIG and LGM temporal agreement between approaches was observed. For the most recent period (middle Holocene) temporal and spatial agreement were observed.

Given the congruence between approaches, our study highlights the following conclusions:

1.- Distribution dynamics of endemic and non-endemic species result in similar patterns throughout long-term climatic fluctuations such as Glacial/Interglacial cycles and Marine Isotope Stages.

2.- More divergent patterns can be observed during episodes of profound climatic alterations such as LGM and HS1.

3.- Endemic species are highly resilient and remained in the core area during periods of strong alteration of temperature and precipitation.

4.- Non-endemic species are sensitive to decreases of temperature, being displaced to Central America to track climates compatible with their tolerance ranges.

This study represents to our knowledge the first insight into the magnitude of ecological alteration of aquatic ecosystems during different past climatic scenarios in the northern Neotropical region. Further studies may therefore consider refining the spatial and temporal resolutions of the analyses and incorporate additional lines of evidence such as molecular data. The understanding of historical species dynamics can help to generate strategies for the protection of the biota which can be highly threatened by the future emergence of non-analogous climates.

Author contributions.

SC, LMG and KN designed species distribution models and carried them out. LGM and SW provided data for model parametrization and validation. LP, PE, MB, JC provide data on fossil assemblages for the periods LGM and middle Holocene. SC, LMG and AS prepared the manuscript with contributions from all co-authors.

Competing interests.

The authors declare that they have no conflict of interest.

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Figures

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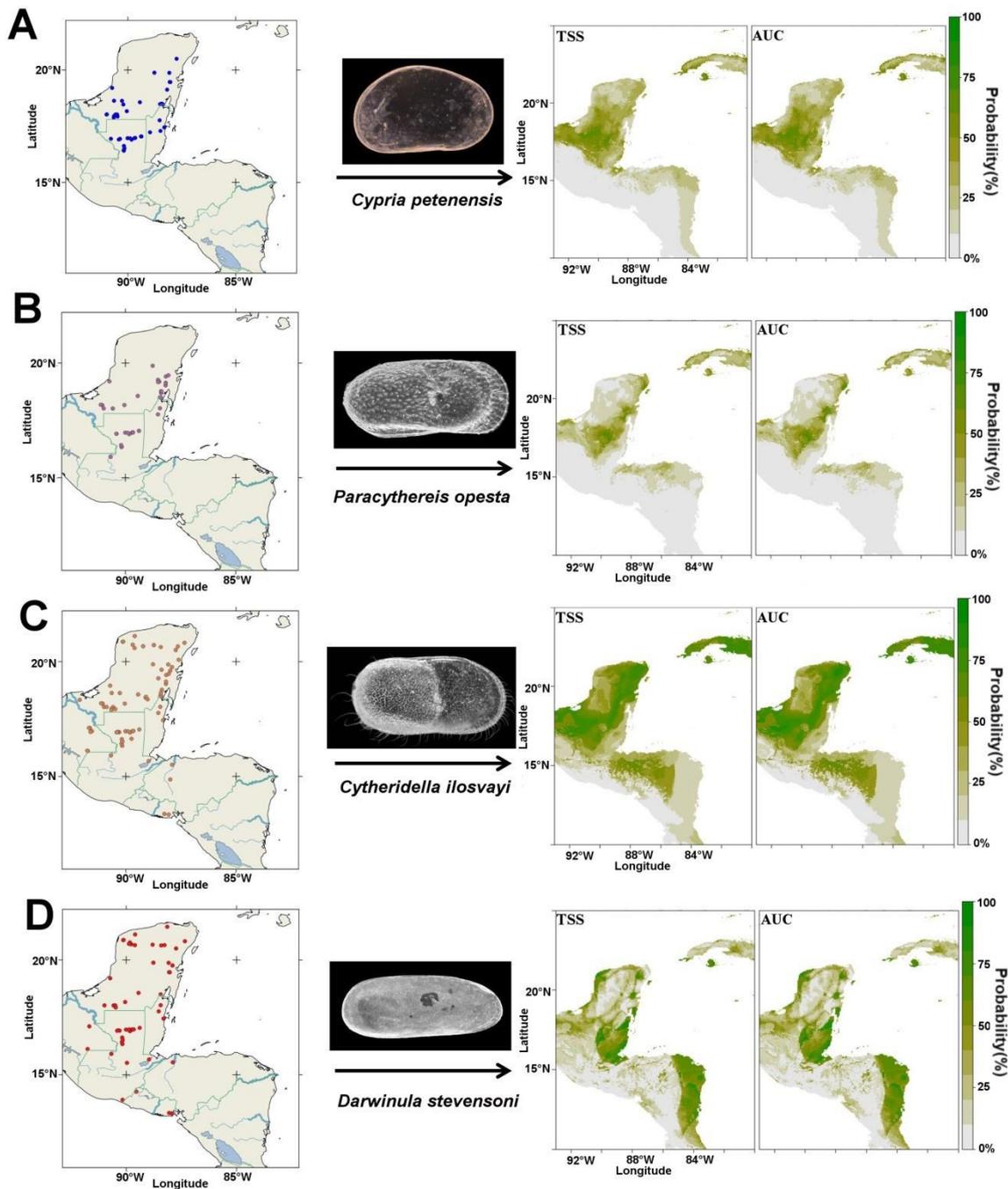
Figure 1 Current ostracode species distributions and predicted distribution based on species
niche modeling and two statistical evaluations: true skill statistic (TSS) and area under the
receiver operating characteristic curve (AUC). A) *Cypria petenensis*, B) *Paracythereis
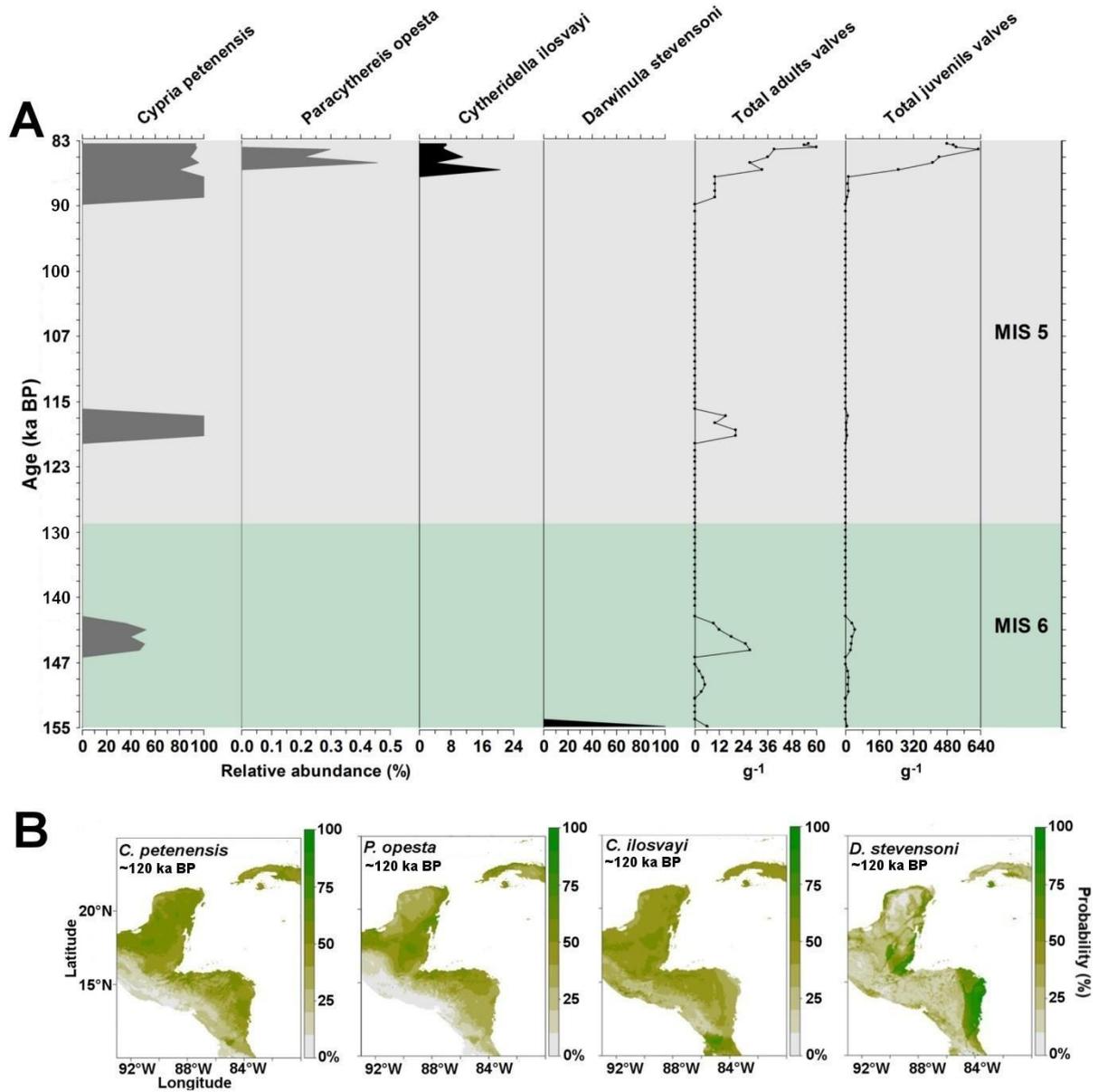opesta*, C) *Cytheridella ilosvayi*, D) *Darwinula stevensoni.*

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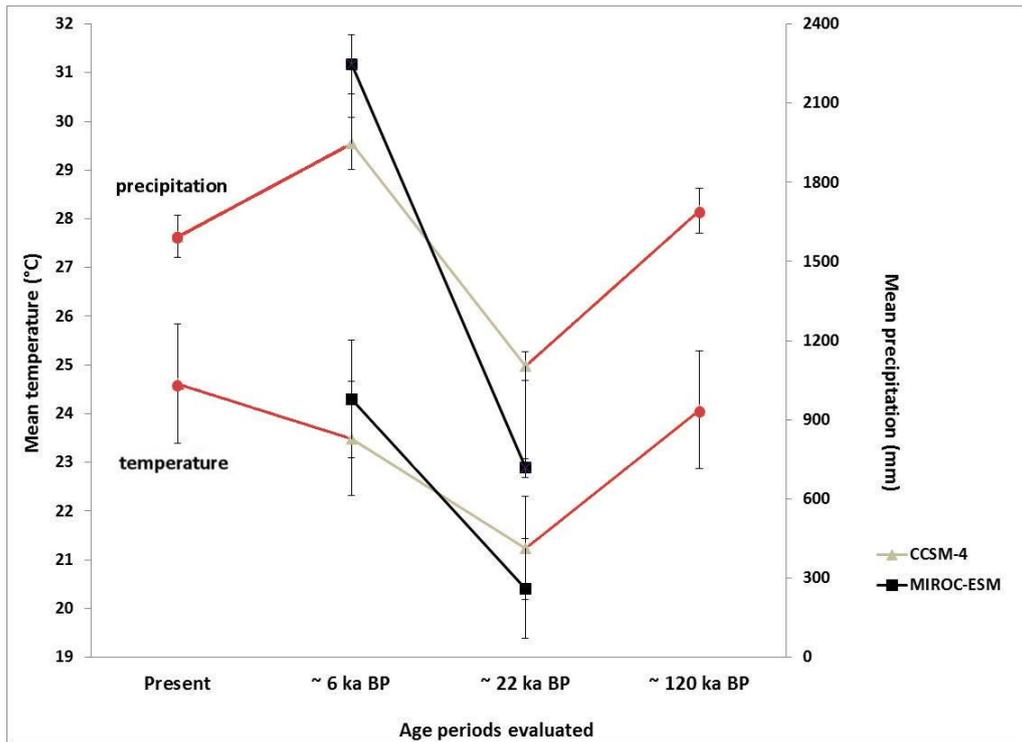
Figure 2. Estimated mean annual temperature and mean annual precipitation values for ~120 ka BP, ~22 ka BP, ~6 ka BP and present. Estimates for ~22 and ~6 ka BP were based on general circulation models CCSM-4 (gray line) and MIROC-ESM (black line).

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Figure 3. Fossil record of the period 155-83 ka BP and species niche modeling results for the ~120 ka BP (representing Last Interglacial climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni.* A) Fossil record of four ostracode species from core PI-1 in Lake Petén Itzá, and B) Maps from niche modeling, showing the probability of species distributions.
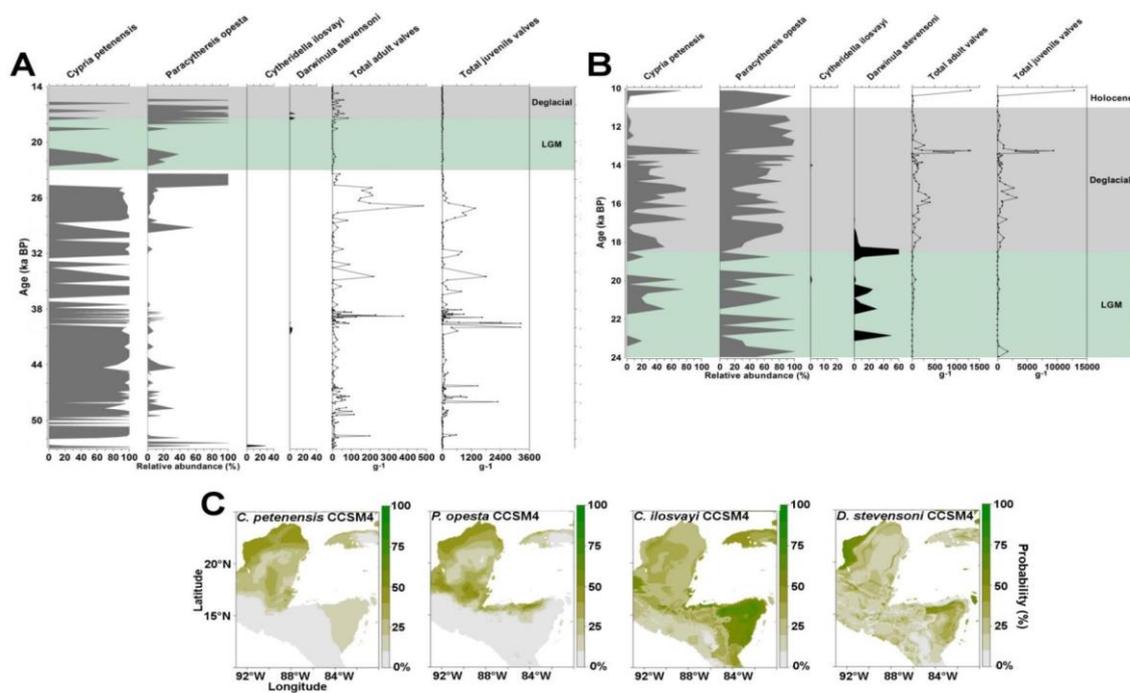
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Figure 4. Fossil record of the period 53-10 and species niche modeling results for the ~22 ka BP (representing Last glacial maximum climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. Fossil ostracode record from Lake Petén Itzá. A) Core PI-2 for the period 53-14 ka BP, B) Core PI-6 for the period 24-10 ka BP (taken from Pérez et al. 2011) and C) map showing the probability of species distributions based on the CCSM-4 climate model.
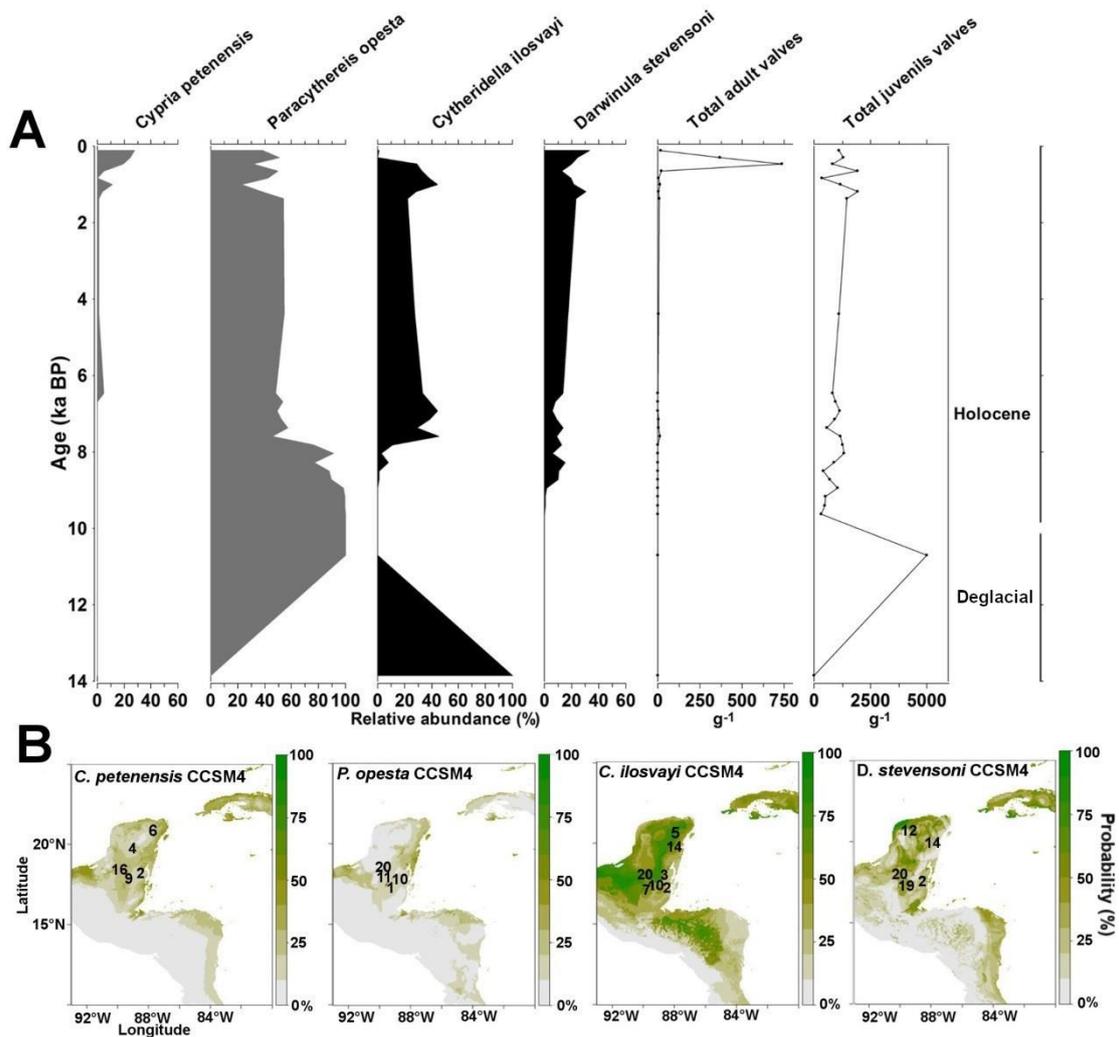
Figure 5. Fossil record of the last 14 ka and species niche modeling results for the ~6 ka BP (representing Mid-Holocene climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. A) Ostracode fossil record from core Petén Itzá 22-VIII-99. B) Map showing the probability of suitable species distribution based on the CCSM-4 climate model. Numbers in maps represent regional fossil records. Numbers correspond to those in Supplementary material, Table S1.
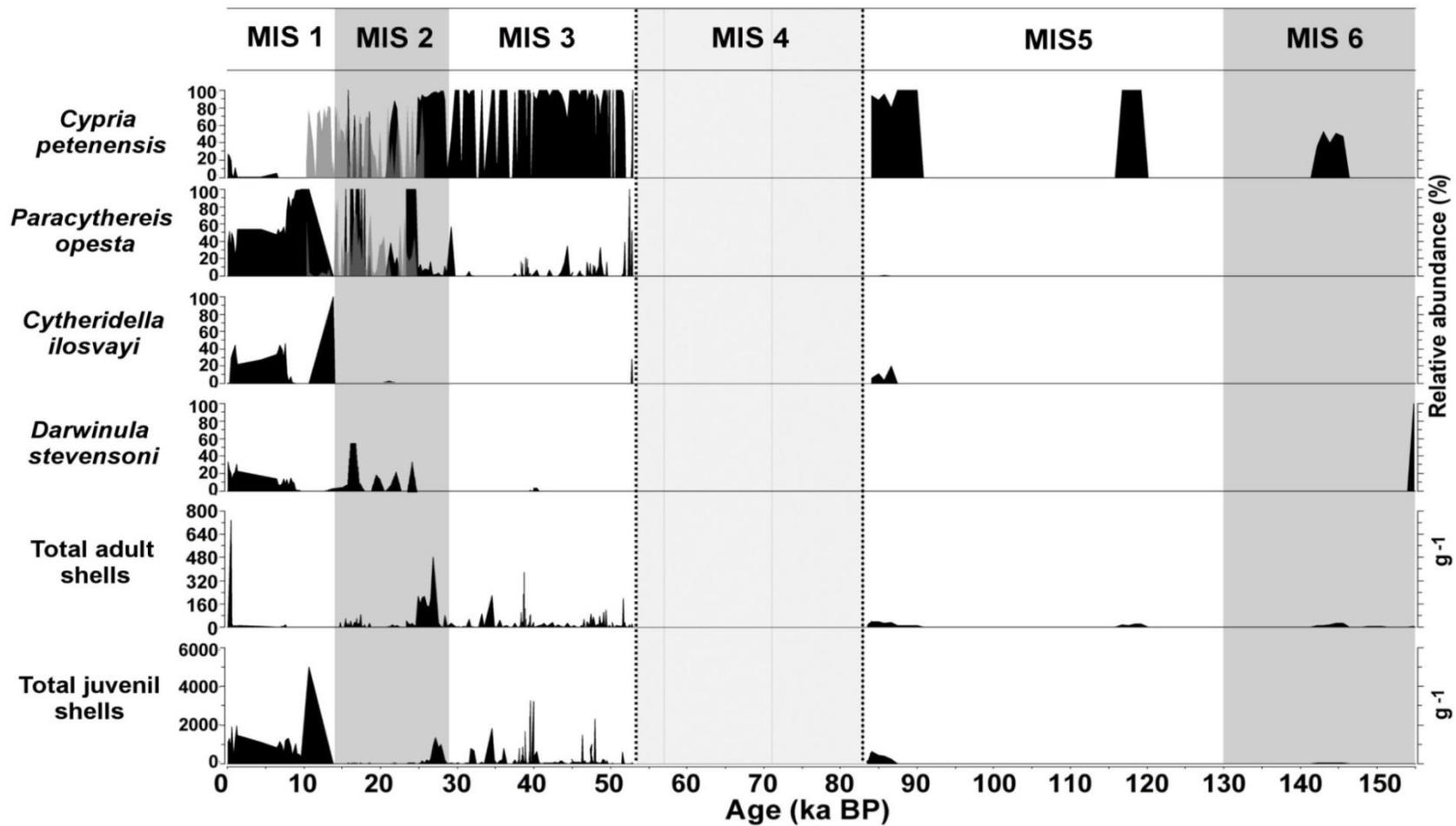
Figure 6. Master profile of the fossil ostracode record during Marine Isotope Stages of the last 155 ka in Lake Petén Itzá. Zone delimited by dashed lines represents a period of data absence. Gray peaks during the period of 24-10 represent results from core PI-6, whereas black peaks during the same period represent results from core PI-2
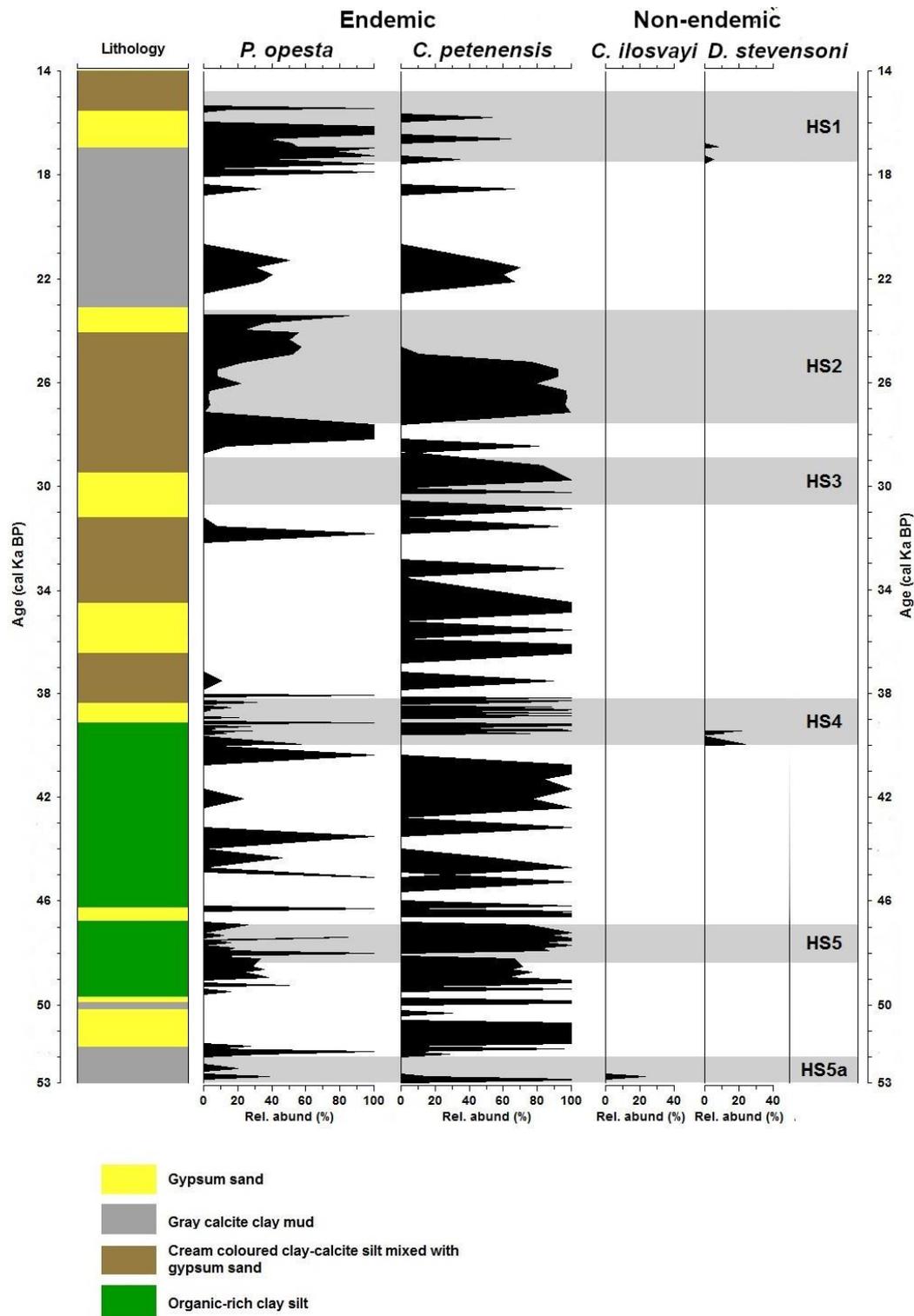
Figure 7. Fossil record of two endemic (*Paracythereis opesta* and *Cypria petenensis*) and two non-endemic (*Cytheridella ilosvayi* and *Darwinula stevensoni*) ostracode species during the period 53-14 ka BP. Gray horizontal bars represent temporal extent of Heinrich Stadials (HS5a-HS1). Modified from Cohuo et al., (2018).

1 **Table 1.** Ostracode species niche modeling, input data and evaluation scores. Variables of

2 importance (mean of 10 evaluation runs) and evaluation model performances based on true

3 skill statistic (TSS) and area under the receiver operating characteristic curve (AUC).

4 Variable importance scores ≥ 0.30 are shown in bold.

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Species	Presences	True absences	Variables importance	Evaluation of ensemble models		
				TSS	AUC	KAPPA
Cytheridella ilosvayi	79	112	BIO 1 (0.05), BIO 2 (0.03), BIO 3 (0.05), **BIO 4 (0.46)**, BIO 7 (0.13), BIO 12 (0.05), **BIO 15 (0.30)**	0.47	0.81	0.49
Darwinula stevensoni	61	130	BIO 1 (0.05), **BIO 2 (0.39),** BIO 3 (0.01), BIO 4 (0.10), BIO 7 (0.01), BIO 12 (0.11), BIO 15 (0.11)	0.58	0.85	0.56
Paracythereis opesta	37	154	BIO 1 (0.10), BIO 2 (0.24), BIO 3 (0.10), BIO 4 (0.06), BIO 7 (0.14), BIO 12 (0.08) **BIO 15 (0.48)**	0.72	0.91	0.71
Cypria petenensis	49	142	BIO 1 (0.10), **BIO 2 (0.30),** BIO 3 (0.09), BIO 4 (0.09), BIO 7 (0.15), BIO 12 (0.03), **BIO 15 (0.31)**	0.63	0.89	0.56

6 Abbreviation are as follows: annual mean temperature (BIO1), mean diurnal range (BIO2),

7 isothermality (BIO 3), temperature seasonality (BIO4), temperature annual range (BIO7),

8 annual precipitation (BIO12), precipitation seasonality (BIO15).

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