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

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20 **Abstract**

22 We evaluated how ranges of four endemic and non-endemic aquatic ostracode

23 species changed in response to long-term (glacial-interglacial cycles) and abrupt

24 climate fluctuations during the last 155 ka in the northern Neotropical region. We

25 employed two complementary approaches, fossil records and species distribution

26 modeling (SDM). Fossil assemblages were obtained from sediment cores PI-1, PI-2,

27 PI-6 and Petén-Itzá 22-VIII-99 from Petén Itzá Scientific Drilling Project, Lake Petén

28 Itzá, Guatemala. To obtain a spatially resolved pattern of (past) species distribution, a

29 downscaling cascade is employed. SDM´s were reconstructed for the Last Interglacial

30 (~120 ka BP), the Last Glacial Maximum (~22 ka BP) and the middle Holocene (~6 ka

31 BP). During glacial/interglacial cycles and Marine Isotope Stages, modeled paleo-

32 distributions and paleo-records show nearly continuous presence of endemic and

33 non-endemic species in the region, suggesting negligible effects of long-term climate

34 variations on aquatic niche stability. During periods of abrupt ecological disruption

35 such as Heinrich Stadial 1 (HS1), endemic species were resilient, remaining within

36 their current areas of distribution. Non-endemic species, however, proved to be more

37 sensitive. Modeled paleo-distributions suggest that the geographic range of non-

38 endemic species changed, moving southward into Central America. Due to the

39 uncertainties involved in the downscaling from the global numerical to the highly

40 resolved regional geospatial statistical modelling, results can be seen as benchmark

41 for future studies using similar approaches. Given relatively moderate temperature

42 decreases in Lake Petén Itzá waters (~5ºC) and persistence of some aquatic

43 ecosystems even during periods of severe drying in HS1, our data suggest 1)

44 existence of micro-refugia and/or 2) continuous interaction between central

45 metapopulations and surrounding populations, enabling aquatic taxa to survive

46 climate fluctuations in the northern Neotropical region.

47

48 **Keywords:** Climate change, freshwater ostracodes, Neotropics, fossil records,

49 species niche modelling.

50

51 **1 Introduction**

52 Climate changes are quasi-cyclical natural processes that continuously influence

53 ecosystem dynamics and shape biological diversity worldwide. During the Late

54 Quaternary, climate fluctuations such as glacial/Interglacial cycles, are recognized as

55 the main drivers responsible for past species extinctions (Martínez-Meyer et al.,

56 2004; Nogués-Bravo et al., 2008), speciation events (Peterson and Nyári, 2008;

57 Solomon et al., 2008), delimitation of refugia (Hugall et al., 2002; Peterson et al.,

58 2004) and development of migration pathways (Ruegg et al., 2006; Waltari and

59 Guralnick, 2009) for both plants and animals. In the northern Neotropics, which

60 include southern Mexico, Central America and the Antilles, late Quaternary climate

61 inferences based on climatic simulations with global climate models (GCMs)

62 (Hijmans et al., 2005) and reconstructions from marine and lacustrine sedimentary

63 sequences (Hodell et al., 2008; Pérez et al., 2011,2013; Escobar et al., 2012) have

64 revealed climate fluctuations related to temperature and precipitation, especially

65 during transitions between glacial and interglacial episodes, and during climate

66 pulses such as the Last Glacial Maximum (LGM) and Heinrich stadials (HS) (Correa-

67 Metrio et al., 2012b). In the Neotropics, controls of climate fluctuations are related to

68 orbital forcing and internal component variations, such as the position (north-south) of

69 the inter tropical convergence zone (ITCZ), strength of Atlantic meridional overturning

70 circulation (AMOC) and changes in Caribbean surface water temperature (Cohuo et

71 al., 2018). Alterations in these features have produced temperature decreases in a

72   range of 3 -5ºC, although some estimations suggest decreases up to 10ºC relative to

73   present and large reductions in precipitation, particularly during HS, when most lakes

74   in the region dried completely (Cohuo et al., 2018). Correa-Metrio et al. (2014) found

75   evidence for rapid climate change in terrestrial environments during HS, which was

76   associated with major ecological and biological shifts (Loarie et al., 2009; Burrows et

77   al., 2011; Sandel et al., 2011). Correa-Metrio et al. (2012a, b,2014) found that plant

78   survival in the northern Neotropical region during HS required migrations to refugia.

79   The climatically driven pace and magnitude of changes in aquatic environments can,

80   however, vary considerably relative to effects in terrestrial environments (Sandel et

81   al., 2011; Litsios et al., 2012; Bonetti and Wiens, 2014). It therefore remains

82   uncertain how aquatic species responded to past climate alterations.

83   To evaluate past biogeographic dynamics of northern Neotropical inland aquatic

84   species, we used freshwater ostracodes (bivalved microcrustaceans) as a model

85   group, and two complementary approaches (1) fossil records (Dawson et al., 2011;

86   McGuire and Davis, 2013) and (2) species distribution models (SDM) (Elith and

87   Leathwick, 2009; Nogués-Bravo et al., 2009; Veloz et al., 2012; Maguire et al., 2015).

88   Ostracodes were selected because they possess one of the best fossil records in the

89   region since the Late Quaternary (Pérez et al., 2011, 2013) and have demonstrated

90   to be sensitive to climatic variation (at modern and past). Given their intermediate

91   role on trophic chains (Valtierra-Vega and Schmitter-Soto, 2000; Bergmann and

92   Motta, 2005; Cohuo et al., 2016), changes in their abundances and assemblage

93   composition can also reflect changes in primary production and higher trophic levels.

94   Paleorecords provide true evidences for the presence of a species within the past, at

95   resolutions ranging from decadal to millennial scales, but in absence of a denser

96   spatial network, this approach is usually limited to the local scale (Maguire and

97   Stigall, 2009; Dawson et al., 2011). Species distribution models are based on the

98   combination of georeferenced species occurrences with environmental information to

99   characterize the range of climate tolerance that a species inhabits (Guisan and

100   Thuiller, 2005; Maguire et al., 2015). By using multiple time periods, species

101   occurrences across different climatic scenarios can be projected to a certain degree

102   (Elith and Leathwick, 2009; Svenning et al., 2011).

103   Most important limitations and uncertainties of SDMs are the according forcing data

104   such as GCMs and the statistical algorithms employed. For instance, simulations of

105   tropical Atlantic climates remain deficient in many climate models due to incomplete

106   characterization of the vertical structure of tropospheric water vapor and humidity. As

107   a consequence, the simulation of temperature and precipitation gradients is afflicted

108   with a high degree of uncertainty in GCM's, especially across regions with irregular

109   and complex topography (Solomon et al., 2010). Statistical algorithms and data

110   parametrization also add another level of uncertainty in the downscaling cascade,

111   including the structure of past surface fields such as topography, vegetation structure

112   and coastline. Moreover, the usage of statistical algorithms for the geospatial

113   mapping also includes uncertainties that are implicitly included in the results (Chen et

114   al., 2010; Neelin et al., 2010).

115   The combination of paleorecords and SDM's, provides a unique opportunity to obtain

116   quantitatively and potentially high-resolution reconstructions of past species

117   dynamics at local and regional scale during past climate fluctuations in the northern

118   Neotropical region.

119   In this study, we addressed three overarching questions: 1) Did past climate changes

120   since 155 ka BP (Hodell et al., 2008; Correa-Metrio et al., 2012a, b, 2014; Cohuo et

121   al., 2018) have profound consequences for aquatic ecosystem stability in the

122   northern Neotropics? 2) Did endemic and non-endemic (widespread) species

123   respond in the same way to climate shifts? 3) Did refugia exist, and if so, what was

124   their spatial distribution?

125   **2 Methods**

126   **2.1 Study area and sampling of modern species**

127   Our study area is the northernmost northern Neotropics, an area that extends from

128   southern Mexico to Nicaragua (Fig.1). We sampled 205 aquatic ecosystems during

129   2010–2013, including *cenotes* (sinkholes), lakes, lagoons, crater lakes, maars,

130   permanent and ephemeral ponds, wetlands, and flooded caves. Sampled systems

131   are located at elevations from ~10 to ~4000 m a.s.l., and conductivity ranged from

132   0.1 to 3500 µS cm^{-1}. Most aquatic systems were shallow with a mean depth < 10m,

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

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

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

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

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

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

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

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

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

142   dissections were carried out in 3% glycerine. Shells were mounted on

143   micropaleontological slides. Dissected appendages were mounted in Hydromatrix®

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

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

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

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

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

149   1870), which are widely distributed (non-endemic) on the American continent (Fig.

150   1C, D).

151   **2.2 Sediment cores from Lake Petén Itzá and regional paleo-records**

152

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

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

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

156   and Petén-Itzá 22-VIII-99 were used. Core chronologies and sampling methods can

157   be found in Kutterolf et al. (2016) and Mueller et al. (2010), respectively. Sample

158   resolution (20 cm) in each core represents ~5 ka (Mueller et al., 2010). Ostracode

159   separation methods and counting can be found Cohuo et al. (2018). We looked at

160   near-continuous ostracode fossil occurrences in the sediments over the last 155 ka.

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

162   We also compiled fossil data for our target species from 19 other studies in the

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

164   (Supplementary material, Table S1). These studies were restricted to the LGM and

165   middle Holocene.

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

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

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

169 version 1.5 (Juggins, 2007).

2.3 Species niche modelling (SNM): modern projections and reconstruction of past distributions

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

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

174 2010). Given the ecological preferences of the species, we used seven environmental

175 variables related to temperature and precipitation, as they have been shown to have

176 the strongest relationships with ostracode distribution: 1) mean annual temperature, 2)

177 mean diurnal temperature range, 3) isothermality (day-to-night temperature oscillation

178 relative to summer-to-winter), 4) temperature seasonality, 5) annual temperature

179 range, 6) total annual precipitation, and 7) precipitation seasonality, all available from

180 the WorldClim database (Hijmans et al., 2005; http://www.worldclim.org). Variables of

181 importance were analyzed to identify those with greatest influence on each ostracode

182 species distribution.

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

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

185 climate databases such as the Global Historical Climatology Network (GHCN) and the

186 Food and Agricultural Organization of the United Nations (FAO). Grids had a spatial

187 resolution of 30-arc second. Although modern climatic data is generated at very high

188 resolution, one should note that modelling of tropical climate and circulation is still

189 afflicted by a comparatively high degree of uncertainty, especially the realistic

190 simulation of the hydrological cycle and precipitation. In this context, the purpose of

191 the study is also to investigate how far differences in profound background climatic

192 changes during Glacial-Interglacial periods are responsible for lateral and/or vertical

193 changes in ecological niches of the respective species.

194 Past species distributions were investigated using climate conditions inferred for

195 three time periods: ~120 ka BP (last interglacial), ~22 ka BP (Last Glacial Maximum

196 [LGM]) and ~6 ka BP (middle Holocene). For environmental data corresponding to

197 ~120 ka BP (Otto-Bliesner et al., 2006), grids have a spatial resolution of 30-arc

198 seconds, which represents ~1 km^2 in the northern Neotropical region. Environmental

199 conditions at ~22 and ~6 ka BP were obtained from downscaled paleoclimatic

200   simulations forced with the coarsely resolved output fields of two global circulation

201   models (GCMs), the MIROC-ESM 2010 (Watanabe et al., 2011) and CCSM4 (Gent

202   et al., 2011).

203   These GCMs were selected because they yield slightly varying temperature and

204   differences in precipitation fields (Fig. 2). At ~22 ka BP, the MIROC-ESM model

205   shows colder and drier conditions in the region than does the CCSM4 model (Fig. 2).

206   At ~6 ka BP, the CCSM4 model simulates slightly cooler and drier conditions than

207   does the MIROC-ESM model (Fig. 2). These differences enable assessment of model

208   uncertainty with respect to global climate simulations.

209   The target grids at the lower end of the downscaling cascade have a spatial resolution

210   of 2.5-arc minutes, which represents ~5 km^2 in the study area. For all periods, grids

211   with global information were trimmed to match the extent of our study area. The SDM

212   toolbox (Brown, 2014), implemented in Arc GIS, was used for this purpose.

213   The modeling framework was constructed using five presence/absence-based

214   algorithms because of true species absences in our database. We used the

215   Generalized Linear Model (GLM) (McCullagh and Nelder, 1989), the Generalized

216   Additive Model (GAM) (Hastie and Tibshirani, 1990), the Generalized Boosting Model

217   (GBM) (Ridgeway, 1999), Maximum Entropy (MAXENT) (Tsuruoka, 2006) and the

218   Surface Range Envelope (SRE) (Busby, 1991). The first three algorithms, GLM, GAM

219   and GBM are regression-based models, which are flexible to handle a variety of data

220   responses types (linear and non-linear) and are less susceptible to overfitting than

221   other algorithms such as multivariate adaptive regression splines (MARS) (Guisan et

222   al., 2002; Franklin, 2010). MAXENT is a general-purpose machine learning method

223   which predicts a species probability occurrence by finding the distribution closest to

224   uniformity (maximum entropy), it requires previous knowledge of the environmental

225   conditions at known occurrence localities (Elith et al., 2011). The SRE algorithm is an

226   envelope-type method that uses the environmental conditions of locations of

227   occurrence data to profile the environments where a species can be found (Araujo

228   and Peterson 2012). All these modelling techniques are at different degree limited by

229   several numerical factors, such as missing values, outliers, sampling size, overfitting

230   and interaction between predictors. Special attention therefore must be paid to

231   produce reliable models which maximizes the agreement of the predicted species

232   occurrences with the observed data (Guisan et al., 2002; Franklin, 2010). In most

233   cases the combination of methods (e.g. GLM and GAM) is recommended to assess

234   the robustness of according results of individual models (Guisan et al., 2002).

235   For our study, settings for all modeled techniques, such as the number of trees,

236   number of permutations, iteration depths, Bernoulli distribution normalization and

237   node-size, follow George and Thuiller (2013). Records were split randomly into a

238   training (calibration) (70%) and a test (validation) (30%) dataset, with 10 replications

239   for each model type. A total of 50 models (5 algorithms and 10 replications) were

240   generated for each ostracode species and time period. All projections were evaluated

241   using three statistical approaches, to reduce uncertainty in species niche models: 1)

242   The true skill statistics (TSS), (2) the area under the receiver operating characteristic

243   curve (AUC) and (3) Cohen's Kappa statistics (Thuiller et al., 2009, 2015). For all

244   algorithms, best-fit model runs above critical values (TSS values >0.4, AUC >0.7 and

245   KAPPA >0.4) were used to construct consensus maps for each modeling technique.

246   Final maps were constructed using an ensemble of all techniques. The combination

247   of methods reduces the effect of inter-model variability and uncertainties that arise

248   from using single algorithms (Araújo and New, 2007; Marmion et al., 2009; Thuiller et

249   al., 2009). The final distribution maps thus indicate areas simulated by most modeling

250   techniques. All calculations were done using the 'biomod2' v.3.1-64 package (Thuiller

251   et al., 2015), implemented in R v.3.2.1 software (R Development Core Team, 2015).

252   **3 Results**

253

254   **3.1 Northern Neotropical paleorecords, species permanence and displacement**

255

256   Records of the period corresponding to the Last Interglacial (130-115 ka BP), were

257   obtained from core PI-7 (155-83 ka BP). Abundances of our four target species were

258   generally low, with <60 adult shells gr^{-1}, and frequencies (relative abundances) varied

259   considerably (Fig. 3). The endemic *C. petenensis* was the most frequent species (Fig.

260   3). *Paracythereis opesta* and *C. ilosvayi,* which are bottom-dwelling organisms, were

261   recovered only from sediments deposited ca. 87-85 ka BP, where high abundances of

262   *C. petenensis* were observed (Fig. 3). *Darwinula stevensoni* showed a sole

263   occurrence at ~155-153 ka BP.

264   Records of the Last Glacial and Deglacial were obtained from Lake Petén Itzá core PI-

265   2 (Fig. 4A) and published data from core PI-6 (Fig. 4B) (Pérez et al., 2011). Pérez et

266   al. (2011) found nearly continuous presence of endemic species in core PI-6 during

267   the interval 24-10 ka BP. Gaps of millennial duration are, however, evident for the

268   periods 24–22 and 13–10.5 ka BP. The record from PI-2 shows a complementary

269   pattern to that of PI-6, because species presence in PI-2 coincided with species

270   absence in core PI-6. *Cypria petenensis* in the PI-2 record, for example, shows high

271   abundances at the onset of the LGM (23-21 ka BP), and *P. opesta* displays high

272   abundances around 22 and 19 ka BP (Fig. 4A). Thus, the two records suggest

273   continuous presence of endemic species in Lake Petén Itzá during both the LGM and

274   Deglacial.

275   Non-endemic species show intermittent distributions in both the PI-2 and PI-6 cores

276   (Fig. 4A, B). *Darwinula stevensoni* was recorded exclusively at ca. 23, 22-20, and 19-

277   18 ka BP, the latter at the onset of the Deglacial. Similarly, *Cytheridella ilosvayi* was

278   present in very low abundances during two short episodes at about 20 and 14 ka BP.

279   We recorded low abundances of both species during the LGM (<250 adult shells g^{-1}),

280   compared to periods immediately before and after, when temperatures are thought to

281   have been warmer. For example, during the Deglacial, abundances were always >250

282   adult shells g^{-1}.

283   Fossil records from the middle Holocene were obtained from core Petén-Itzá 22-VIII-

284   99 and eleven regional studies (Fig. 5A). The record from core Petén-Itzá 22-VIII-99,

285   retrieved from 11.5 m water depth, shows that endemic species were present

286   continuously during the last 6.5 ka (Fig. 5A). Most regional records came from

287   *cenotes* and lakes on the Yucatán Peninsula (Supplementary material, Table S1). All

288   fossil records show that endemic species were spatially distributed throughout the

289   current ranges of extant populations (Fig. 5B).

290   For non-endemic species, regional fossil records from the middle Holocene revealed

291   their presence ranging from the northern Yucatán Peninsula to northern Guatemala

292   and Belize (Supplementary material, Table S1). Core Petén-Itzá 22-VIII-99 highlights

293   an almost continuous presence of *C. ilosvayi* in the lake, characterized by high

294   abundances, except for the period 11-8.5 ka BP, when the species was absent (Fig.

295   5A). *Darwinula stevensoni* was present continuously during the last 9 ka, but in the

296   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

297
298
299

300 For the 205 aquatic ecosystems sampled, 145 had at least one of the target species

301 present: *C. petenensis, P. opesta, C. ilosvayi* and *D. stevensoni*. Forty-nine systems

302 contained *C. petenensis*, 37 had *P. opesta*, 79 were inhabited by *C. ilosvayi*, and 61

303 contained *D. stevensoni*. Analysis of variables of importance showed that

304 environmental variables with the greatest influence on species distribution are

305 precipitation seasonality and mean annual temperature (Table 1). For individual

306 species, however, variables received different scores, indicating that each species

307 optimal climate niche is controlled by a particular combination of variables (Table 1).

308 Diagnostic tests of the reconstructions (TSS, AUC and Kappa) show good

309 performance for all algorithms and periods evaluated (Table 1). There were,

310 however, differences in predictive accuracy within species. Modeled distributions of

311 endemic species have the highest evaluation scores (AUC =0.8, TSS=0.49,

312 Kappa=0.45). Non-endemic species models (AUC=0.75, TSS=0.46, Kappa=0.46)

313 have slightly lower values, but also fall within the acceptable range.

314 Reconstructions for the period ~120 ka BP suggest very broad distributions of

315 endemic taxa, as climate enabled the species to expand their ranges. Probability

316 values, however, were relatively low (<80%) (Fig. 3B). For the non-endemic species,

317 reconstructions for ~120 ka BP show different areas of climatic suitability, with species

318 presence probabilities reaching 60%. Zones of higher probability (>80%) are

319 dispersed throughout the region. The most extensive zones of species distribution

320 suitability are located along the Caribbean coast of the Yucatán Peninsula and in

321 northern Guatemala (Fig. 3B).

322 Inferences for endemic taxa distributions at ~22 ka BP, based on the CCSM4 model,

323 suggest that these species remained in the core area, but that they may have been

324 displaced somewhat to the northern portion of the Yucatán Peninsula (Fig. 4C). This

325 estimate has probability values of >75%. The MIROC-ESM model suggests areas of

326 distribution similar to those presented by the CCSM4 model, but slightly more

327 restricted areas for *C. petenensis* and more widespread areas for *P. opesta*.

328 Probability values were low in this model (<65%) (Supplementary material, Fig. S1).

329 Models for non-endemic species reveal fragmented and discontinuous distributions

330 (Fig. 4C). At ~22 ka BP, corresponding to the LGM, both the CCSM4 and MIROC-

331 ESM models suggest that non-endemics moved northward on the Yucatán Peninsula

332 to the Gulf of Mexico (>65% probability), and/or were displaced southward to Central

333 America (85% probability) (Fig. 4C; Supplementary material, Fig. S1).

334 For ~6 ka BP, the CCSM4 model suggests discontinuous areas of distribution on the

335 Yucatán Peninsula (Fig. 5B) for endemic species, whereas the MIROC-ESM shows

336 more continuous distributions, particularly along the eastern portion of the Peninsula

337 (Supplementary material, Fig. S1). For non-endemic species, the CCSM4 and

338 MIROC-ESM models show very similar patterns. Extensive regions of climatic

339 suitability were identified for *C. ilosvayi*, but those with higher probability are located

340 along the Caribbean Coast (Fig. 5B; Supplementary material, Fig S1). For *D.*

341 *stevensoni*, areas of maximum probability are discontinuous. Maximum probability

342 was found at isolated regions such as the southern part of the northern Yucatán

343 Peninsula, Belize and eastern Honduras (Fig. 5B).

344

345 **4 Discussion**

346

347 **4.1 Congruence between paleo-records and modeled paleo-distributions of**

348 **freshwater ostracodes in the northern Neotropical region**

349 Our study highlights the fact that accuracy and congruence between paleo-records

350 and modeled paleo-distributions of freshwater ostracodes in the northern Neotropical

351 region was influenced by multiple factors such as climate model used, modeling

352 algorithm employed, sediment core characteristics and target species.

353 For instance, distribution models and modelling cascade were characterized by high

354 degree of uncertainty with regard of precipitation and temperature estimations of

355 climate models (GCMs). This limited the full estimation of spatial distribution of target

356 species, especially during older periods such as LIG and LGM were fossil evidence

357 (spatial and temporal) was scarce.

358 The simulation of precipitation of GCMs is afflicted with high degrees of uncertainties,

359 because the vertical structure of stratospheric water vapor and humidity profile have

360 large biases, especially in the tropics (Gettelman et al., 2010). This implies that GCMs

361 commonly reproduce large-scale pattern of precipitation with high confidence but

362 models tend to underestimate the magnitude of precipitation change at regional or

363 local scale (Stephens et al., 2010). Similarly, GCMs temperature estimations in the

364 tropics may display large biases, because changes in climate drivers of continental

365 temperature of the northern Neotropics such as Atlantic sea surface temperature and

366 the Atlantic warm pool, are usually underestimated (Liu et al., 2013). Simulations of

367 temperature variations during LGM, for example, tend to overestimate cooling in

368 tropical regions (Kageyama et al., 2006; Otto-Bliesner et al., 2009).

369 In our study, reconstructed maps based on MIROC-ESM and CCSM4 models,

370 simulate slightly different areas of distribution for the target species. This is associated

371 to differences in precipitation and temperature estimations between models. The most

372 important difference between their respective reconstructions pertains to the extent of

373 suitable areas of distribution of the species, being generally broader in MIROC-ESM

374 model than in CCSM4 model.

375 The scarcity of fossil records also limited the full reconstruction of distribution

376 dynamics of species, especially during LIG and LGM, because records were obtained

377 only from Lake Petén Itzá and were relatively scarce. The period 24-14 ka BP, was

378 highly informative, because the comparisons between cores PI-2 and PI-6, and

379 specifically, the compensation effect between them (the presence of species in a core

380 in periods were absences were determined in the other), highlight that gaps in the

381 fossil record may be related to core location in the lake, shell preservation and

382 individual species ecology and not only by species absence. This therefore, suggest

383 that short gaps, lasting less than 10 ka cannot be considered evidence for species

384 absence.

385 In general, the comparison between species distribution models and paleorecords

386 shows a quite high degree of similarity. This is especially evident for the middle

387 Holocene as the individual SMD output of the target species were compared with the

388 fossil records at regional scale. In all cases, SDMs reconstructions shows

389 distributional areas where fossil records were recovered. This congruence may be

390 supported by the agreement between estimations of temperature in climate models

391 and paleorecords.

392

393 **4.2 Endemic and non-endemic species responses during long-term climatic**

394 **fluctuations: Glacial/Interglacial cycles and Marine Isotope Stages**

395 Paleoclimate inferences derived from Lake Petén Itzá sediments suggest that

396 Glacial/Interglacial cycles in the northern Neotropical region did not have profound

397 consequences with respect to the spatial distribution of isotherms in terrestrial

398 environments (Hodell et al., 2008; Pérez et al., 2011; Escobar et al., 2012; Pérez et

399 al., 2013). Most paleoclimate studies in the region based in different proxies such as

400 ostracods, pollen, and δ^{18}O fluid inclusion data from speleothems suggest that

401 temperatures during the last glacial and start of the deglacial may have been up to

402 5ºC lower than today (Correa-Metrio et al., 2012a, b; Arienzo et al., 2015; Cohuo et

403 al., 2018), although some estimations suggest a temperature depression of about

404 10ºC compared with modern records (Hodell et al., 2012; Grauel et al., 2016).

405 Precipitation was affected more profoundly, but not consistently during glacial-

406 interglacial cycles and likely fluctuated in response to changes in local atmospheric

407 circulation. For instance, the position of the Hadley cell and ITCZ, together with

408 climate forcing, such as Heinrich Stadials, seem to drive precipitation fluctuation

409 locally. During the LGM, for example, humid conditions has been estimated to the

410 region (Cohuo et al., 2018).

411 Our results, however, suggest that temperature fluctuations affected aquatic species

412 associations to a higher degree compared to reductions in precipitation (changes in

413 lake water chemistry), because presence/absence of species and fluctuations in total

414 abundances match periods of temperature change, rather than times of lake level

415 shifts.

416 Endemic and non-endemic species responded similarly to Glacial and Interglacial

417 cycles and transitions. Fossil records from Lake Petén Itzá sediment cores PI-1, PI-2,

418 PI-6, and Petén-Itzá 22-VIII-99 reveal that endemic species were almost continuously

419 present during the last 155 ka. Short gaps, lasting less than 10ka were not considered

420 evidence for species absence.

421 Non-endemic species show patterns of expansion and contraction that track

422 temperature fluctuations. Modeled paleo-distributions and paleo-records show that

423 distributions of non-endemic species were widespread during the LIG and

424 fragmented during the middle Holocene, when climates were warmer. During the Last

425 Glacial, non-endemic species were absent or sporadically present. This may result in

426 response to lower temperatures characterized the LG. Modeled paleo-distributions

427 for the LGM also show that non-endemic species were displaced from their current

428 ranges toward the northern Yucatán Peninsula and/or southward toward Central

429 America, where a warm climate likely persisted. This scenario suggests migrations of

430 regional magnitude, as species were lost from areas such as southern Mexico and

431 northern Guatemala but persisted within their current range of distribution in

432 fragmented populations, such as areas of southeast Honduras and northeast

433 Nicaragua.

434 The presence of endemics and absence of non-endemic species during the LGM,

435 reveal a clear ecological signal, which may be associated to the degree of adaptation

436 to ecological niches. Endemic species seem to be highly resilient to long-term natural

437 disturbances, whereas non-endemic demonstrated to be more sensitive. There is

438 increasing evidence that biological communities, particularly terrestrial taxa, display

439 strong resilience in the face of natural and human disturbances in the northern

440 Neotropical region. Hurricane impacts, widespread pre-Columbian agricultural

441 activities, and decadal-to-centennial climate changes are recognized as main

442 disrupters of Holocene ecosystem composition and function in the region. Such

443 perturbations, however, did not severely and permanently alter plant associations

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

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

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

447 350yrs after strong deforestation by pre-Columbian agriculture (Bush and Colinvaux,

448 1994). Similarly, the rain forest in Guatemala recovered from Mayan alterations in a

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

450 demonstrated rapid recovery time after hurricane impacts, species compositions

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

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

453 Johnson and Winker, 2010).

454

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

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

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

458 155 ka. High abundance of ostracodes, which belong to intermediate trophic levels,

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

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

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

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

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

464 inferred for this period.

465 Marine Isotope Stages (MISs), which describe shorter periods of (marine) climate

466 variability (cooling and warming) than terrestrial Glacial/Interglacial cycles, were also

467 used to evaluate the distribution dynamics of aquatic species. During MISs, ostracode

468 composition remained relatively constant, even across MIS boundaries (Fig. 6).

469 Sediments from Lake Petén Itzá that correspond to warmer periods MIS3 (57-29 ka

470 BP) and MIS1 (14 ka BP to present) were characterized by abundant fossils. MIS2

471 (29-14 ka BP) shows lower species abundances (total adult and juvenile valves), likely

472 related to persistent cold temperatures. The absence of *Cytheridella ilosvayi* during

473 most of MIS2 illustrates the sensitivity of non-endemics to cool temperatures (Fig. 6).

474 Similar to Glacial/Interglacials in terrestrial environments, during MISs, northern

475 Neotropical endemic species showed high resilience to changes between cold and

476 warm phases, whereas non-endemic species proved to be more sensitive to cold

477 periods, especially the LGM.

478 **4.3 Species responses during abrupt climate shifts, and refugia for aquatic taxa**

479 Fossil records from Lake Petén Itzá suggest that the periods of strongest climatic

480 fluctuations during the last 155 ka BP in the northern Neotropics occurred around 85

481 ka BP (Mueller et al., 2010) and Heinrich Stadials (Correa-Metrio et al., 2012b; Cohuo

482 et al., 2018). Those episodes were characterized by dramatic decreases in lake level,

483 suggesting intense aridity in the region. Lowest estimated temperatures (5-10 ºC

484 lower than today) for the entire record correspond to HS1.

485 Correa-Metrio et al. (2013) estimated high climate change velocity in the region during

486 HS1, which produced large changes in terrestrial plant communities. Correa-Metrio et

487 al. (2012b, 2014) estimated that one of the consequences of such ecological

488 instability was the substantial migration of tropical vegetation and development of

489 refugia. The high velocity of climate change inferred for the northern Neotropical

490 region is, however, opposite to trends observed elsewhere in the tropics, which

491 suggest that high biodiversity and endemicity are associated with low climate change

492 velocities and high species resilience (Sandel et al., 2011). It remains uncertain how

493 climate change velocity during period of abrupt climate change affected aquatic

494 communities in the northern Neotropical region. It is also unclear whether aquatic taxa

495 were as dramatically affected as local terrestrial species during these abrupt episodes,

496 or if they simply displayed high resilience.

497 We analyzed the HS1 structure in detail, because that was the period of coldest

498 temperatures and extreme drought during the last 85 ka (Mueller et al., 2010; Correa-

499 Metrio et al., 2012a; Cohuo et al., 2018). Mueller et al. (2010) estimated that Lake

500 Petén Itzá water level decreased by ~50 m during that period, which would imply that

501 lakes in the region with maximum depths <50 m, dried completely.

502 Modeled paleo-distributions suggest that with respect to temperature fluctuations

503 during HS1, conditions remained suitable for tropical species (especially endemics)

504 across large areas of the Yucatán Peninsula and in northern Central America. We

505 assume that lakes that held water during HS1 served as "refugia" for aquatic taxa, as

506 temperature apparently did not limit species distributions (Cohuo et al., 2018).

507 Systems such as *cenotes* and lakes that are not directly dependent on precipitation to

508 maintain water level, but are instead controlled by large subterranean aquifers (Perry

509 et al., 2002; Schmitter-Soto et al., 2002; Vázquez-Domínguez and Arita, 2010) may

510 serve as "refugia" for aquatic species, enabling native species to remain in the region

511 during periods of low rainfall. To date, it remains uncertain whether lakes and *cenotes*

512 (approximately 7,000 in the Yucatán Peninsula) held water during HS1, and little is

513 known about their spatial distribution. Isolated water bodies (refugia) may explain the

514 high percentage of endemicity and micro-endemicity (species distributed in a single or

515 limited group of lakes) for aquatic taxa on the northern Yucatán Peninsula (Mercado-

516 Salas et al., 2013). Species that inhabited such systems may have remained isolated

517 and adapted to specialized environmental niches.

518 Deevey et al. (1983) studied sediment cores from Lakes Salpetén (z_{max} = ~30 m) and

519 Quexil (z_{max} = ~30 m), Guatemala, and inferred that most lakes, including *cenotes,* in

520 the northern Neotropics dried out during the Deglacial because of the hydrological

521 sensitivity of the region. They also found that most lake sediment cores from the

522 region bottom out at ~8 ka BP, which means that the lakes probably first filled in the

523 early Holocene, in response to wetter conditions and rising sea level, which raised the

524 local water table. The authors therefore suggested that only large lakes in the region,

525 with maximum depths >50 m (e.g. Petén Itzá, Macanché, Atitlán, Coatepeque,

526 Ilopango) held water during the dry Deglacial, but possessed water chemistry much

527 different from today, which limited habitats for aquatic species.

528 This second scenario favors the hypothesis of central populations (meta-populations)

529 in one or more large lakes, which enabled species exchange with surrounding aquatic

530 environments, thereby preventing species losses in small populations by demographic

531 stochasticity. The two scenarios are not mutually exclusive, and it is possible that both

532 account for the success of aquatic tropical taxa through periods of abrupt or prolonged

533 climate fluctuations. Lake Petén Itzá may have played an important role for aquatic

534 species survival and dispersal in the northern Neotropical region, because it held

535 water for at least the last 400 ka (Kutterolf et al., 2016).

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

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

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

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

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

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

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

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

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

545 <1km^2, and deep waters >10m) and large lakes as Petén Itzá (>120m deep), dramatic

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

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

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

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

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

551 **5 Conclusion**

552 Our study integrates species distribution models and paleorecords to reconstruct

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

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

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

556 circulation models MIROC-ESM and CCSM4 simulations related to precipitation and
557 temperature. Although these uncertainties can be considered as systematic errors, it
558 remains uncertain whether the lower-end simulations based on SDMs generated in
559 this study, fully reconstruct suitable areas of distribution of aquatic species, especially
560 because in tropical regions the larger biases on simulated values of precipitation and
561 temperature have been estimated.

562 Most important limitations of paleorecords relate to the scarcity of fossil evidence
563 spatially and temporally, especially for the older periods evaluated. Low abundances
564 in ostracodes were associated to species ecological preferences, core location and
565 preservation processes. The integration of fossil evidence from two long cores of the
566 Lake Petén Itzá was highly informative as the full range of temporal
567 presence/absence of the target species were recovered.

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

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

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

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

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

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

583 This study represents to our knowledge the first insight into the magnitude of
584 ecological alteration of aquatic ecosystems during different past climatic scenarios in
585 the northern Neotropical region. Further studies may therefore consider refining the

586   spatial and temporal resolutions of the analyses and incorporate additional lines of

587   evidence such as molecular data. The understanding of historical species dynamics

588   can help to generate strategies for the protection of the biota which can be highly

589   threatened by the future emergence of non-analogous climates.

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609   Author contributions.

610   SC, LMG and KN designed species distribution models and carried them out. LGM

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612   provide data on fossil assemblages for the periods LGM and middle Holocene. SC,

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614   Competing interests.

615   The authors declare that they have no conflict of interest.

616

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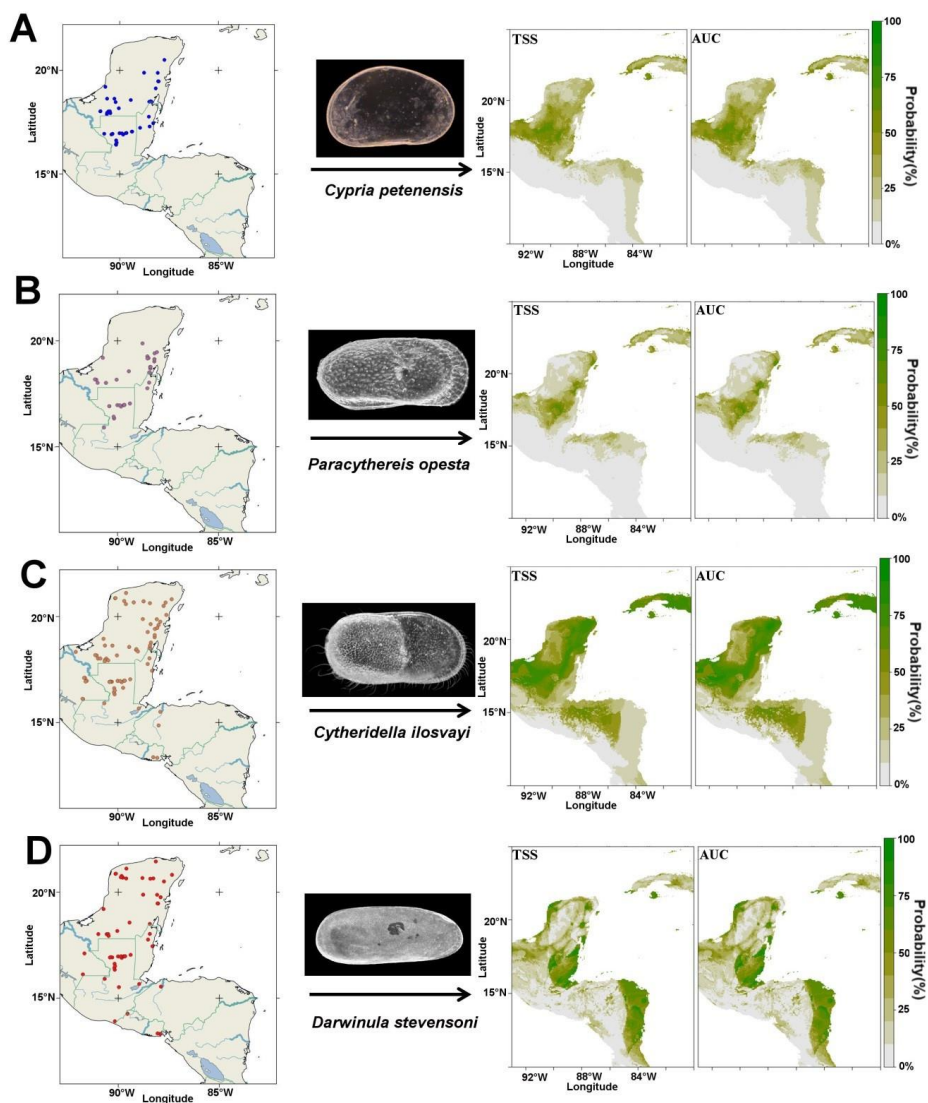
911 **Figures**

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913 **Figure 1** Current ostracode species distributions and predicted distribution based on species

914 niche modeling and two statistical evaluations: true skill statistic (TSS) and area under the

915 receiver operating characteristic curve (AUC). A) *Cypria petenensis*, B) *Paracythereis*

916 *opesta*, C) *Cytheridella ilosvayi*, D) *Darwinula stevensoni*.

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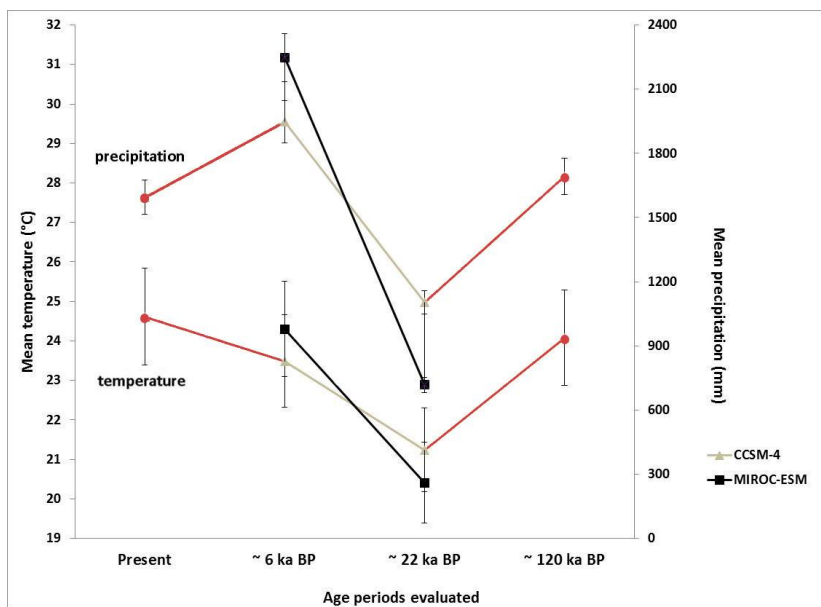
Figure 2. Estimated mean annual temperature and mean annual precipitation values for ~120

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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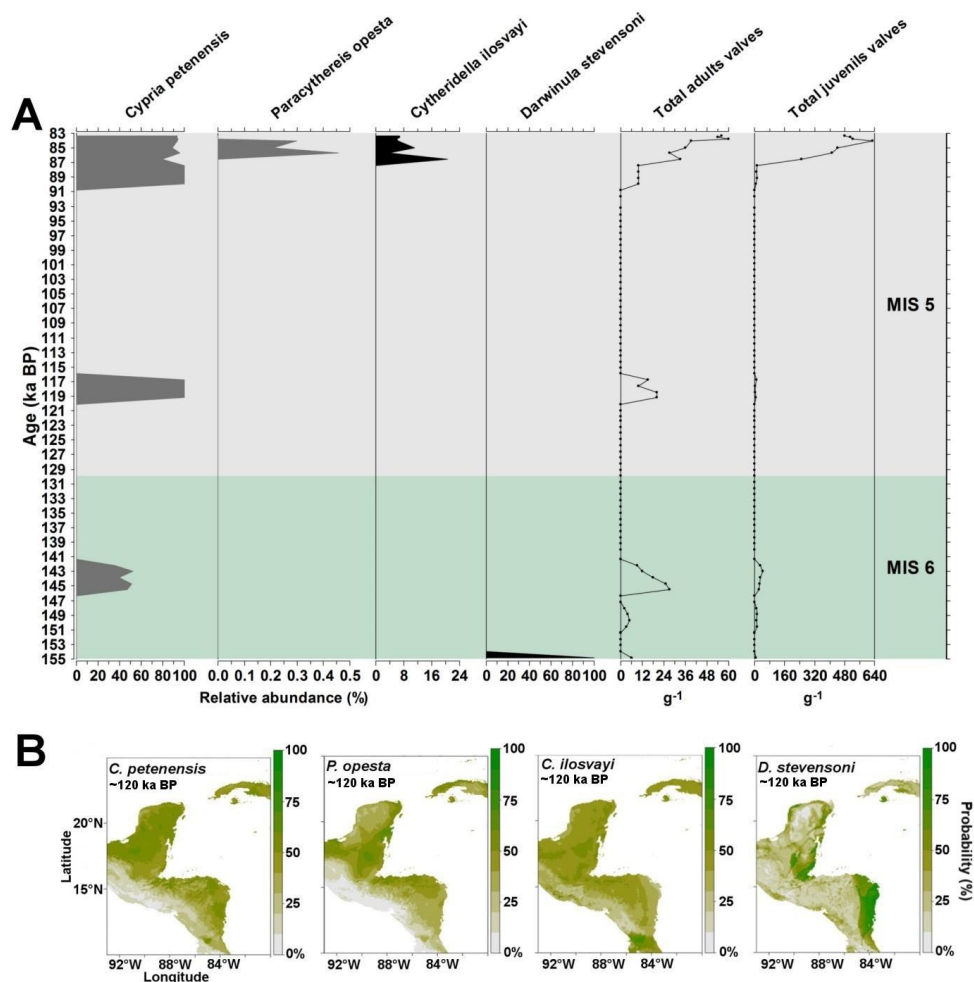
Figure 3. Fossil record of the period 155-83 ka BP and species niche modeling results for the ~120 ka BP (representing Last Interglacial climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. A) Fossil record of four ostracode species from core PI-1 in Lake Petén Itzá, and B) Maps from niche modeling, showing the probability of species distributions.
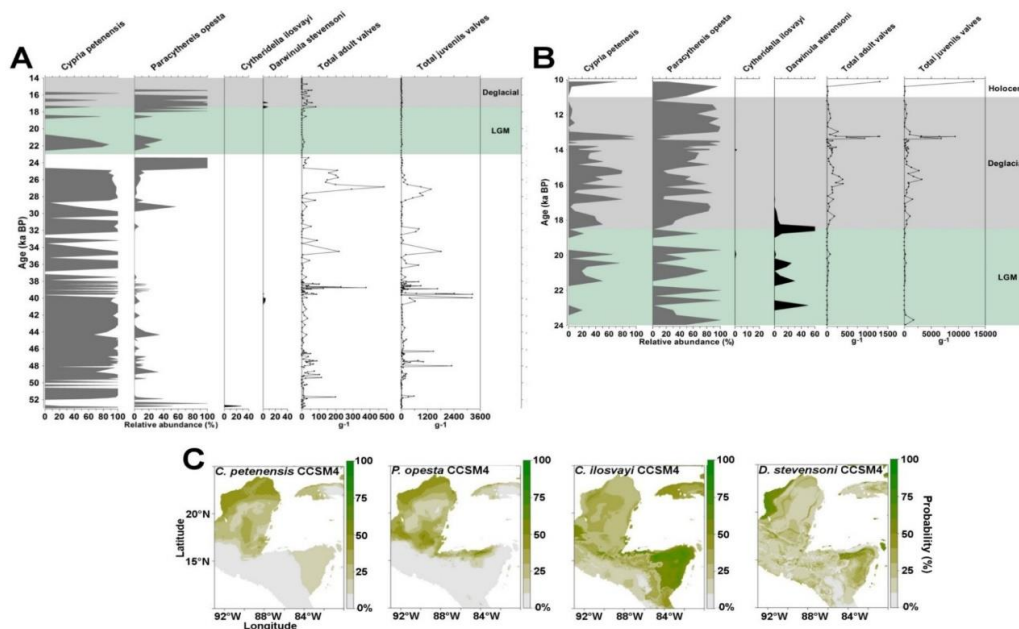
Figure 4. Fossil record of the period 53-10 and species niche modeling results for the ~22 ka BP (representing Last glacial maximum climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. Fossil ostracode record from Lake Petén 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.
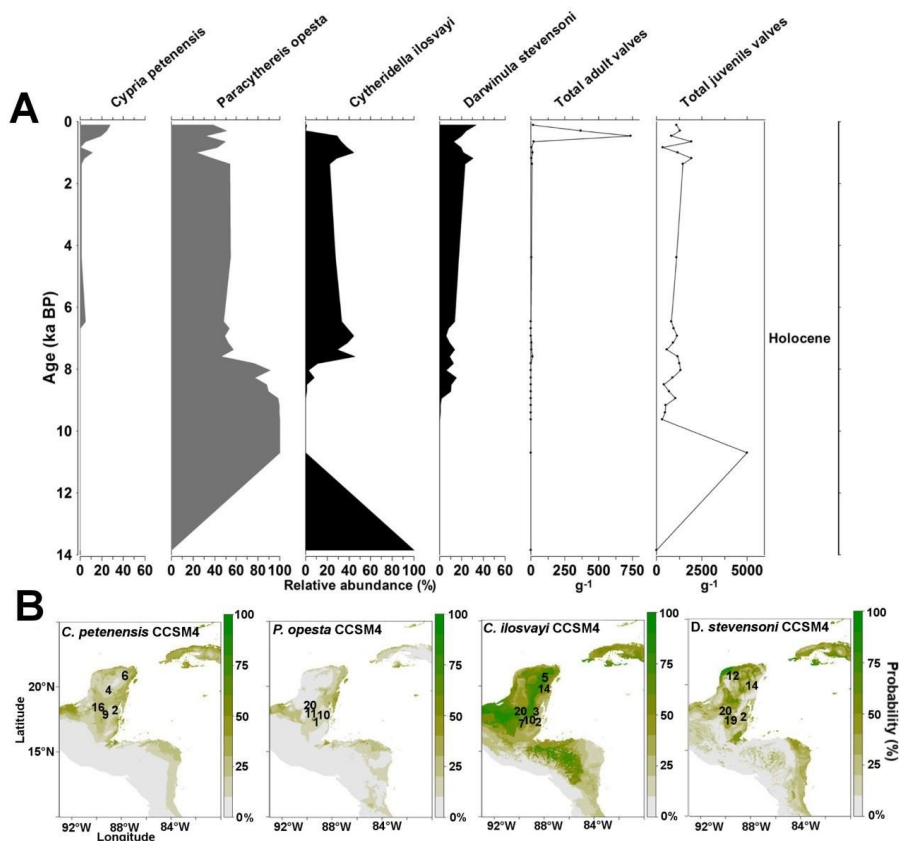
Figure 5. Fossil record of the last 14 ka and species niche modeling results for the ~6 ka BP (representing Mid-Holocene climate) for four ostracode species: *Cypria petenensis, Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. A) Ostracode fossil record from core Petén Itzá 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.
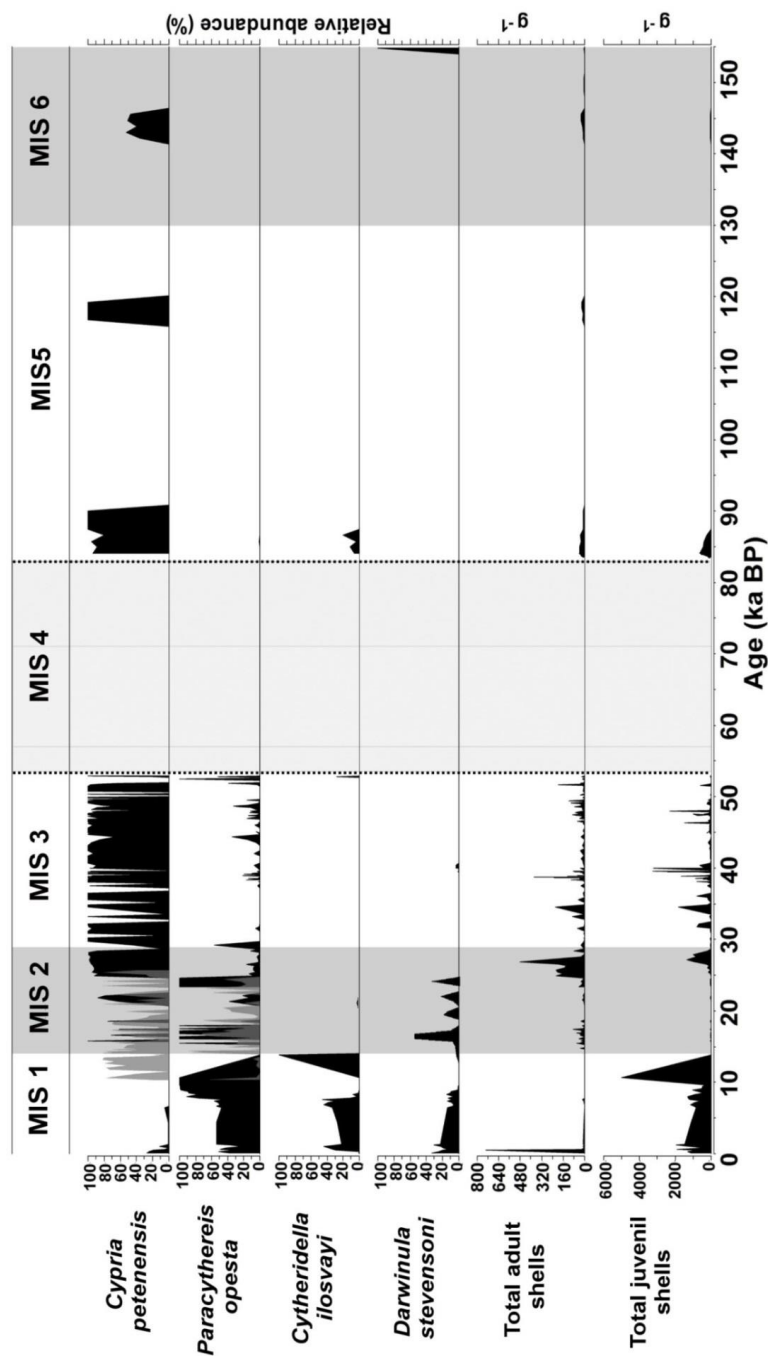
Figure 6. Master profile of the fossil ostracode record during Marine Isotope Stages of the last 155 ka in Lake Petén Itzá. Zone delimited by dashed lines represents a period of data absence. Gray peaks during the period of 24-10 represent results from core PI-6, whereas black peaks during the same period represent results from core PI-2.

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.

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