Tropical freshwater ostracodes as environmental indicators across an altitude gradient in Guatemala and Mexico

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Abstract: Detailed knowledge of species ecological preferences and robust taxonomy of paleobioindicators are prerequisites for accurate paleoclimate and paleoenvironmental studies. This study aims to expand the knowledge of modern, Neotropical freshwater ostracode fauna, across an altitudinal gradient from the karst lakes in the lowlands of El Petén, Guatemala (100-500 m.a.s.l.), to the mid-elevation lakes of the Lacandón forest (500-1 000 m.a.s.l.), to the higher-altitude lakes of Montebello, Chiapas, Mexico (1 000-1 500 m.a.s.l.). Eighteen ostracode species were identified in 24 lakes. Ostracodes were absent in Lakes Amarillo and Lacandón (mid-altitude), and San Diego (lowlands); probably explained by a structural difference of habitats and species interactions. Statistical analysis indicated that the most abundant species, *Cypridopsis vidua* (O.F. Müller, 1776)*, Cytheridella ilosvayi* Daday, 1905, *Pseudocandona antilliana* Broodbakker, 1983*, and Darwinula stevensoni* (Brady & Robertson, 1870) have a continuous distribution along the entire altitudinal gradient. Some species display more restricted distributions, determined by temperature, precipitation and conductivity. For example, *Eucypris* sp. is restricted to the lowlands, *Vestalenula* sp. and *Cypria* sp. were found only at middle elevations. Species diversity is slightly greater in lakes at middle altitudes ($H_{average}$ = 1.09) than in water bodies in the lowlands ($H_{average}$ = 0.94) and in cooler lakes in the highlands ($H_{average}$ = 0.94), suggesting that mid-elevation lakes have a high potential for harboring microrefugia. Locally weighted scatterplot smoothing (LOESS regressions) provided ecological preference information for the four most frequent and widely distributed species, with respect to temperature, conductivity, bicarbonate (HCO_3^-) concentration, precipitation, and pH. *Darwinula stevensoni* suggest an association more to cooler temperatures and lower conductivities proving its high tolerance range. *Cypridopsis vidua* is associated with warm and low-rainfall environments, such as recorded in the lowlands of Guatemala, and can be used as a paleobioindicator of vegetated littoral zones, because we found

it always associated to this section of lakes. *Cytheridella ilosvayi* show preferences for warm and humid conditions, whereas *P. antilliana* prefer colder and humid environments. Such quantitative-ecological information will improve ostracode-based paleoenvironmental reconstructions in Southern Mexico and Northern Guatemala. In addition, our approach serves as a model for future paleoecological studies that employ other aquatic bioindicators, such as testate amoebae, cladocerans, and chironomids.

Key words: non-marine ostracodes; diversity; ecology; Neotropic.

The Northern Neotropical region displays geologic and geographic complexity. It possesses one of the largest limestone platforms in the world, the karst environment extends from the lowlands of the Yucatán Peninsula to the middle- and high-altitude areas of Chiapas, Mexico (Kueny & Day, 2002; Ford & Williams, 2007; Villanueva, 2011). It is part of the largest continuous forest area left in Mesoamerica, constituting an important North-South ecological gradient (Vester et al., 2007). Due to the rapid ecosystem fragmentation and habitat loss, the area is thus interesting for study of modern and past distribution, diversity and ecology of fauna and flora (O'Brien & Pietraszek-Mattner, 1998; Pielke et al., 2007; Correa-Metrio et al., 2012; Franco-Gaviria et al., 2018). The studied lakes ecosystems from El Petén, Northern Guatemala, to the Lacandón forest and Montebello in Chiapas, Mexico span an altitudinal gradient about 100 to 1 500 m.a.s.l., with a mean annual precipitation range between 1 000 to 3 000 mm/ yr across the lake sites (Moreira et al., 2007). These regions have been listed as RAMSAR sites since 2003 because, they display high biodiversity and are connected hydrologically, which highlights the importance that these lakes play in the recharge of aquifers of the sub-basin (Ramírez, 2007; Kauffer & Villanueva, 2011; Alcocer et al., 2016). In spite of the name of National Parks and RAMSAR sites, the limnological characteristics of the lakes are rare and poorly known (Alcocer et al., 2016), as well as ecological and biogeographical studies (Cohuo, Macario-Gónzalez, Pérez, & Schwalb, 2016). Although such information is needed to develop reliable paleoecological and paleoclimatic reconstructions for the region (Pérez

et al., 2012, 2013; Cohuo et al., 2016; Díaz et al., 2017). Lakes of El Petén in Northern Guatemala have been previously studied probably because of their abundance, size, proximity to tourist attractions like Maya archaeological sites, and more recently, their relatively easy access (Brezonik & Fox, 1974; Deevey, Brenner, Flannery, & Yezdani, 1980; Basterrechea, 1988; Correa-Metrio et al., 2012; Pérez et al., 2013). Some paleolimnological studies have also been carried out in the region and showed that many of the lakes contain complete Holocene sediment sequences (Quexil, Salpetén, Macanché) and a few have deposits that extend well into the Pleistocene. The longest records come from deep Lake Petén Itzá (165 m) (Anselmetti et al., 2006), which appears to have held water for the last 400 ka (Kutterolf et al., 2016). A few limnological, paleoecological and palynological studied have been carried out in the Lacandón forest and Montebello region as well (Alcocer et al. 2016; Vázquez-Molina et al., 2016; Franco-Gaviria et al., 2018).

The modern study of Neotropical non-marine ostracodes ecology across an altitudinal gradient was absent until this moment. Ostracodes (Crustacea: Ostracoda) are crustaceans that are 1.5 mm long and can serve as important bioindicators in modern and paleoecological studies because: 1) they are abundant, sensitive and respond quickly to changes in environmental conditions such as temperature, conductivity and lake stage (Meisch, 2000), 2) they have calcium carbonate (calcite) valves that preserve well in lacustrine sediments, which makes them one of the best taxonomic groups for micropaleontological studies, and

3) their wide distribution and high abundance in the Northern Neotropic make them excellent paleobioindicators of past climate and environment (Canudo, 2002), 4) they also possess one of the oldest and most continuous fossil records (Griffiths & Holmes, 2000), and can thus be used to develop calibrations and infer modern and past climate and environmental conditions in the area (Pérez et al., 2012, 2013).

Therefore, our modern dataset provides ostracod-environment relationships across a broad environmental gradient, from El Petén, Guatemala to Montebello, Chiapas, Mexico. The information generated here revealed species-specific ecological preferences and provided additional environmental information on the importance of temperature and precipitation that was unknown before. Our quantitative data is applicable to reconstruction of paleoecological and paleoclimate conditions across this region, facilitating development of transfer functions to infer past temperature, conductivity and precipitation.

MATERIALS AND METHODS

Study area: El Petén, Northern Guatemala, and the Lacandón forest and Montebello, in Chiapas state, Mexico are located in the Chiapas Plateau and the Gulf Coastal Plain physiographic region, which is part of the Sierra de Chiapas and Guatemala (Villanueva, 2011; Ramírez, 2007). They also correspond to the Grijalva-Usumacinta basin in Northwestern Guatemala and Southeastern Mexico and include 27 lakes. Fifteen lakes are located in El Petén, Guatemala (Yaxhá, Macanché, Oquevix, Oquevix pond, Las Pozas, Subín River, San Diego, La Gloria, Sacpuy, El Rosario, Petén Itzá, Petexbatún, Salpetén, Ixlú River, and Perdida), seven in the Lacandón forest (Yax-há, Ocotalito, Nahá, Amarillo, Lacandón, Metzabok, and T'ziBaná) and five in Montebello (Yalalush, Peñasquito, Esmeralda, Liquidambar, and Balantetic) (Table 1). The different morphometries of most of these systems were formed as a consequence of limestone (carbonate) dissolution. Although,

tectonism has been involved as well, especially in highland lakes (Brenner, Rosenmeier, Hodell, & Curtis, 2002).

The studied regions are located between (15.0° - 17.1° N & 89.4° - 91.8° W), in an altitude range from 100 to 1 500 m.a.s.l. Precipitation varies across the landscape from 1 000 to 3 000 mm/yr (Fig. 1; Table 1). Most of the studied lakes were < 40 m deep, except for three lakes in El Petén: La Gloria (65 m), Macanché (80 m) and Lake Petén Itzá (165 m). Lake Balantetic in Montebello, was the highest (1 466 m.a.s.l.), and Lake Perdida in El Petén, was the lowest (75 m.a.s.l.) (Table 1). In particular, El Petén region lies at an altitude of about 110-500 m.a.s.l., with an annual average precipitation of 1 665 mm and an average annual temperature of 27 °C. Lowest monthly temperature (22 °C) in Petén is registered in January and the highest (30 °C) is in May (Pérez, 2010). The bioclimatic classification of El Petén is warm, subtropical and very humid, subtropical warm (Holdridge, 1975; Manoharan, Welch, & Lawton, 2009; Correa-Metrio et al., 2012). The mid-elevation Lacandón forest lies at an altitude of 500-950 m.a.s.l., and possesses large extensions of evergreen tropical forest, mesophilic mountain forests, coniferous forest, and secondary vegetation (Rzedowski, 2006; Vázquez-Molina et al., 2016). The climate is sub-humid and warm, with an average annual temperature of 21 °C, and an annual precipitation between 1 200 and 3 500 mm (Díaz et al., 2017). The region registers two periods of lower precipitation, between February and May, and between July and August (Kauffer & Villanueva, 2011). The Montebello lakes correspond to the highlands, lying between 1 000 and 1 500 m.a.s.l. The main plant associations are coniferous forests, broadleaf forests, mesophilic mountain forests, riparian vegetation, secondary vegetation and crop areas (Villanueva, 2011). The climate is humid temperate with rain year-round. The mean annual precipitation is 2 500 mm, and the mean annual temperature is about 17 °C. It is highly seasonal, with the coldest and warmest periods from December to February and April to September, respectively

TABLE 1

Location, maximum depth and altitude of the study lakes, located along an altitudinal gradient from middle altitudes to the highlands from Northern Guatemala to Southern Mexico

| Region	Lake	ID	Coordinates °N	°W	Maximum depth [m]	Altitude [m a.s.l.]	maxTempW [°C]	minTempC [°C]	Prec [mm]	PrecWet [mm]	PrecDrie [mm]
Montebello (Highlands)	Balantetic	BAL	16.12	91.78	3	1 466	28.7	10.7	1 961	191	125
	Esmeralda	ESM	16.11	91.72	5	1 463	28.7	10.7	1 961	191	125
	Peñasquito	PEÑA	16.13	91.75	40	1 462	28.7	10.7	1 961	919	125
	Liquidambar	LIQ	16.14	91.78	9	1 456	28.7	10.7	1 961	191	125
	Yalalush	YAL	16.09	91.64	18	1 450	29.4	11.9	2 763	1 288	193
Lacandón forest (Mid-altitudes)	Yax-há	YAXL	16.96	91.59	32	930	30.9	13.8	2 568	1 154	202
	Ocotalito	OCOT	16.95	91.60	23	920	30.9	13.8	2 568	1 154	202
	Nahá	NAH	16.98	91.50	18	830	31.7	14.7	2 648	1 198	198
	Amarillo	AMA	16.98	91.50	9	830	31.7	15.2	2 470	1 079	206
	Lacandón	LAC	17.01	91.58	2	545	32.4	15.2	2 470	1 079	206
	Metzabok	MET	17.03	91.50	20	543	33.9	16.6	2 386	1 052	194
	T'zi BaNá	TZI	17.12	91.57	35	542	32.4	15.2	2 470	1 079	206
El Petén (Lowlands)	Yaxhá	YAX	17.01	89.40	25	219	31.5	17.6	1 350	496	139
	Macanché	MAC	16.97	89.64	80	165	31.2	17.5	1 488	542	144
	Oquevix	OQU	15.00	89.74	10	148	33.7	17.8	922	474	15
	Pond Oquevix	TUM	15.00	89.74	10	148	32.2	17.6	1 970	786	160
	Las Pozas	POZ	16.34	90.18	35	146	32.4	17.8	1 817	735	143
	Subin river	SUB	16.64	90.18	1	141	32.7	17.9	1 824	763	148
	San Diego	DIE	16.92	90.42	8	134	32.7	17.9	1 824	763	148
	La Gloria	GLO	16.95	90.37	64	132	32.7	17.9	1 824	763	148
	Sacpuy	SAC	16.97	90.01	6	122	32.2	18.2	1 677	681	138
	El Rosario	ROS	16.52	90.16	2	117	32.1	17.9	1 814	714	150
	Petén Itzá	PI	17.01	89.85	165	115	32.3	18.3	1 511	596	129
	Petexbatún	PET	16.44	90.19	40	115	32.2	17.6	1 970	786	160
	Salpetén	SAL	16.97	89.67	38	114	31.8	18.0	1 523	578	138
	Ixlú river	IXL	16.97	89.69	0.5	110	31.8	18.0	1 523	578	138
	Perdida	PER	17.06	90.02	4	75	32.7	18.7	1 606	662	128
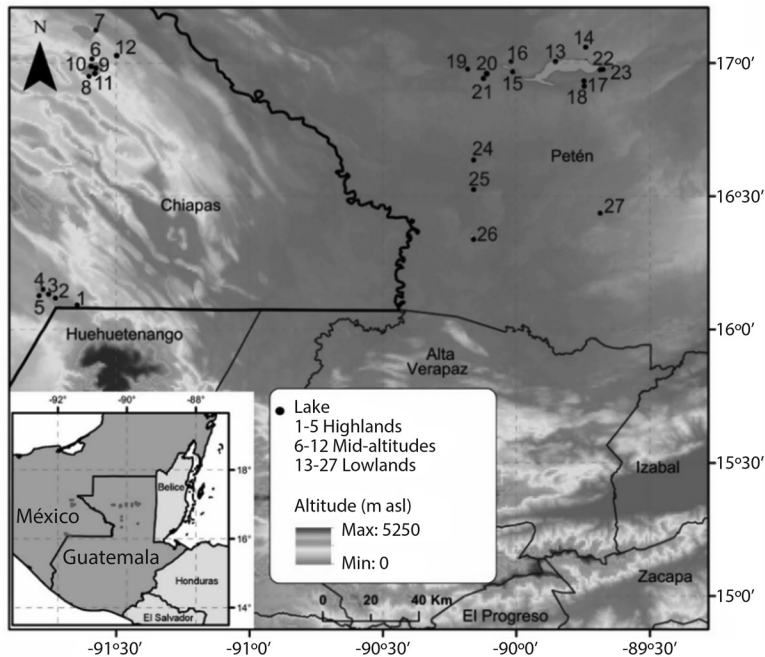
Fig. 1. Altitude and locations of studied karst aquatic ecosystems. Sampled lakes came from three altitudinal ranges: 100-500 m.a.s.l. (El Petén), 500-900 m.a.s.l. (Lacandón forest) and 1 000-1 500 m.a.s.l. (Montebello).

(Rzedowski, 2006; Alcocer et al., 2016; Franco-Gaviria et al., 2018).

Lake name: number of samples per site. 1 Yalalush: 1; 2 Esmeralda:1; 3 Peñasquito: 1; 4 Liquidambar: 1; 5 Balantetic: 1; 6 Lacandón: 2; 7 T'zi Baná: 1; 8 Ocotalito: 2; 9 Naha: 3; 10 Amarillo: 1; 11 Yax-há: 1; 12 Metzabok: 2; 13 Petén Itzá: 16; 14 Perdida: 2; 15 Macanché: 2; 16 Yaxhá: 2; 17 Oquevix: 1; 18 Oquevix pond: 1; 19 Salpetén: 3; 20 La Gloria: 1; 21 San Diego: 2; 22 Ixlú river: 1; 23 Sacpuy: 2; 24 Subín river: 1; 25 El Rosario: 1; 26 Las Pozas: 1; 27 Petexbatún: 3.

Field work: We first collected data on ostracode habitats to generate information on their ecological preferences. We measured physical and chemical variables, the latter including cation and anion concentrations in lake waters. Samples from lakes in the Lacandón forest and Montebello sites were collected in June 2013, during the rainy season. Samples

and *in situ* measurements from waterbodies of El Petén, Guatemala were collected during the dry season between November and February in 2005, 2006 and 2008. The data from El Petén was previously presented by Pérez (2010) and Pérez et al. (2012).

In each water body, temperature, dissolved oxygen, conductivity and pH were measured *in situ* using a Hydrolab Quanta (Chiapas fieldwork) or a WTW multi-parameter probe (Guatemala fieldwork) near sites where surface sediment samples were collected, i.e. in the littoral zone and deepest area. Only a single site, mostly from the littoral zone, was sampled in smaller waterbodies. In larger and deeper lakes samples were taken at different depths. Water depth was determined with a portable depth sounder. Water samples were collected with a Ruttner water sampler for chemical analysis in the laboratory. Water samples for cation analysis were fixed with nitric acid. A total of 56 surface sediment samples were collected, 35 from different depths using an Ekman

grab, and 21 sediment samples were recovered from the littoral zone (0.5-1 m) using a hand net (125-µm mesh). The number of sediment samples collected from each lake is indicated in Figure 1 and Table 2. To guarantee collection of the most recent sediments, only the top 2-3 cm from each Ekman grab were taken and preserved in 95 % ethanol.

Laboratory work (Ostracode analysis): Modern sediment samples were taken to determine ostracode species composition and relative abundances (Appendix 1). From each of the 56 sediment samples, 5 cm^3 were subsampled, sieved using a 63-µm mesh size, and all adult and juvenile ostracode carapaces and valves (broken and intact) were picked using fine brushes and stored on micropaleontological slides. Valves were photographed and measured using scanning electron microscopy (SEM), Hitachi SU 1510 at Laboratorio de Microscopía y Fotografía de Biodiversidad, Instituto de Biología, Universidad Nacional Autónoma de México (Appendix 2, Appendix 3). Carapaces with well-preserved soft parts were stored in Eppendorf vials with 95 % ethanol and then dissected and mounted following methods described by Danielpol et al. (2002). Ostracode species were identified using Pérez et al. (2010, 2012) and Cohuo et al. (2016) descriptions and literature elsewhere. Here we used the most current species names suggested by Cohuo et al. (2016): *Cypria petenensis* (Ferguson et al., 1964) [previously referred as *Physocypria globula* Furtos, 1933], *Cypridopsis vidua* (O.F. Müller, 1776) [previously referred as *C. okeechobei* Furtos, 1936], *Heterocypris putei* Furtos, 1936 [previously referred as *H. punctata* Keyser, 1975], and *Paracythereis opesta* (Brehm, 1939) [previously referred as *Limnocythere opesta* Brehm, 1939].

Water chemistry: Concentrations of major cations (Ca^{2+}, Mg^{2+}, Na$^+$, K$^+$) and anions (HCO$_3^-$, SO$_4^{-2}$, Cl$^-$) were determined in all collected water samples, following standard procedures (APHA, 1995, 1998, 2005; Armienta et al., 2008). Analyses were conducted at Laboratorio de Química Analítica, Instituto de Geofísica, Universidad Nacional Autónoma de México. Oxygen isotope values were measured on water samples from the Lacandón and Montebello lakes using a Picarro L2120-I Isotopic Liquid Water and Water Vapor Analyzer coupled with a Picarro A0211 High Precision Vaporizer and a CTC HTS PAL auto-sampler. Measurements were done at the University of Florida (UF) and results were standardized based on two internal UF water standards (Beta and Gamma) that were calibrated using international standards (V-SMOW, V-SLAP, and V-GISP). Oxygen isotope values on water samples from El Petén lakes were measured at UF using a VG/Micromass (now GV Instruments) PRISM Series II isotope ratio mass spectrometer (Pérez, 2010). All isotope results are reported in standard delta notation relative to Vienna Standard Mean Ocean Water (VSMOW).

Environmental data was standardized using standard deviations. Diversity values were calculated using the Shannon index for each study site, displaying the heterogeneity of communities using: 1) the number of species present (S = richness), and 2) their relative abundances (equitability) (Krebs, 1989; Moreno, 2010). The biological diversity is expressed as e^H/S, where the greater the difference between e^H and S, the less diverse the community is (Jost, 2006).

The most significant variables for the subsequent Canonical Correspondence Analysis (CCA, Fig. 2) were selected using a Principal Component Analysis (PCA, Fig. 3A). PCA included 13 limnological variables (water lake temperature, dissolved oxygen, pH, conductivity, water depth, δ^{18}O, Ca^{+2}, K$^+$, Mg^{+2}, Na$^+$, SO$_4^{-2}$, Cl$^-$, HCO$_3^-$) and five regional environmental variables (maximum air temperature of the warmest month, minimum air temperature of the coldest month, annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter) extracted from the climate data base WorldClim (Fick & Hijmans, 2017) which is often used in species distribution modeling and related ecological modeling techniques. The environmental data were

TABLE 2
Limnological variables from the study lakes in Southern Mexico

Region	Lake	ID	Depth [m]	Water temperature [°C]	O₂ [mg/l]	pH	Conductivity [µS/cm]	Cl⁻ [mg/l]	SO₄⁻²	HCO₃⁻	Ca⁺²	K⁺	Mg⁺²	Na⁺	δ¹⁸O
Highlands	Yalalush	YAL2	18	20.7	4.1	7.5	293	1.7	1.0	189	35	0.2	18.3	0.4	-5.1
	Peñasquito	PEÑA2	40	18.2	0.1	7.0	453	3.0	40.1	234	65	1.0	17.3	2.1	-6.6
	Esmeralda	ESM2	5	22.3	5.1	7.5	358	2.0	5.7	227	45	0.3	20.8	0.5	-6.1
	Liquidambar	LIQ1	0.5	nd	8.6	8.3	485	7.0	111.7	134	73	3.4	15.0	6.6	-10.0
	Balantetic	BAL1	0.5	21.9	6.7	7.5	712	12.1	136.7	285	116	4.5	18.2	14.7	-9.5
Mid-altitudes	Yax-há	YAXL1	0.5	27.3	6.3	7.5	235	2.0	1.3	134	31	0.4	13.5	0.3	-2.3
	Ocotalito	OCOT1	0.5	nd	nd	7.8	275	1.9	1.6	173	27	0.7	21.4	0.3	-3.2
	Ocotalito	OCOT3	7	nd	nd	7.3	279	1.9	3.2	177	29	1.0	20.2	0.4	-2.7
	Nahá	NAH1	0.5	9.1	2.2	5.3	264	1.3	0.6	151	29	0.2	19.7	0.3	-3.8
	Nahá	NAH4	5	24.8	6.4	7.5	nd	nd	nd	nd	nd	nd	nd	nd	-5.6
	Nahá	NAH2	18	21.2	0.6	7.2	483	2.3	1.2	330	54	0.4	32.9	0.5	-5.6
	Amarillo	AMA2	9.1	21.4	0.4	6.9	366	1.9	1.6	242	42	0.5	22.2	0.3	-2.3
	Lacandón	LAC1	1.2	26.2	5.7	7.5	246	1.9	3.1	158	35	0.6	12.6	0.3	-6.7
	Lacandón	LAC2	2	26.0	5.6	7.6	246	1.9	3.1	158	35	0.6	12.6	0.3	-6.7
	Metzabok	MET2	20.1	26.3	4.1	7.5	nd	nd	nd	nd	nd	nd	nd	nd	-5.1
	Metzabok	MET1	0.5	30.5	6.3	7.7	nd	nd	nd	nd	nd	nd	nd	nd	-3.8
	T'zi BaNá	TZI2	35	20.9	0.1	7.0	446	2.3	7.9	279	56	0.5	26.5	0.5	-5.5
Lowlands*	Yaxhá	YAX1	0.5	29.0	7.3	8.7	232	12.8	7.4	118	23	3.7	4.6	9.8	4.3
	Yaxhá	YAX2	25.2	24.8	3.5	8.0	236	12.4	6.5	113	24	3.4	3.3	8.9	4.1
	Macanché	MAC1	0.5	26.8	5.0	8.1	850	41.8	241.8	287	44	5.2	71.3	21.8	3.3
	Macanché	MAC2	60	25.1	1.5	7.9	848	40.5	236.5	274	44	5.6	70.9	20.0	3.3
	Oquevix	OQU1	0.5	31.4	6.9	7.7	238	nd	nd	189	62	nd	4.2	4.0	1.3
	Pond Oquevix	TUM1	0.5	25.9	9.4	9.4	168	nd	nd	85	26	nd	1.4	6.5	5.6
	Las Pozas	POZ1	0.5	29.8	9.0	8.4	292	nd	nd	250	44	nd	30.5	3.4	1.0
	Subín river	SUB1	0.5	26.2	4.2	7.4	720	nd	nd	329	164	nd	12.1	9.2	-3.3
	San Diego	DIE1	0.5	28.6	8.2	8.6	179	nd	nd	140	36	nd	2.7	3.8	1.6
	San Diego	DIE2	8.1	25.4	1.0	7.3	189	nd	nd	134	42	nd	3.4	4.9	1.3
	La Gloria	GLO1	0.5	29.2	8.8	8.6	186	nd	nd	134	40	nd	5.0	5.2	2.4
	Sacpuy	SAC1	0.5	28.8	8.0	8.4	285	nd	nd	171	52	nd	6.2	11.7	2.9

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 67(4): 1037-1058, September 2019

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TABLE 2 (Continued)

Region	Lake	ID	Depth [m]	Water temperature [°C]	O_2 [mg/l]	pH	Conductivity [µS/cm]	Cl^- [mg/l]	SO_4^{-2}	HCO_3^-	Ca^{+2}	K^+	Mg^{+2}	Na^+	$\delta^{18}O$
	Sacpuy	SAC2	5	26.4	4.4	7.8	289	nd	nd	207	52	nd	6.2	11.6	2.9
	El Rosario	ROS1	0.5	28.3	7.6	7.1	1 019	nd	nd	469	133	nd	47.1	2.9	-4.3
	Petén Itzá	PI1	1	27.6	8.9	8.5	533	13.1	158.7	115	59	5.3	18.9	12.1	2.9
	Petén Itzá	PI4	3	27.4	8.9	8.5	532	13.1	159.8	115	66	6.3	20.6	13.4	2.6
	Petén Itzá	PI5	5	27.2	8.9	8.5	532	13.1	161.4	115	75	7.6	22.8	15.0	3.3
	Petén Itzá	PI6	10	27.2	8.9	8.5	531	13.0	149.5	115	73	3.9	20.1	11.4	3.2
	Petén Itzá	PI7	15	27.5	6.8	8.5	531	13.0	153.4	115	80	4.7	21.0	13.2	3.0
	Petén Itzá	PI8	20	26.8	6.5	8.5	529	13.0	159.9	116	82	6.4	21.1	12.6	3.7
	Petén Itzá	PI9	25	26.7	5.9	8.5	534	13.0	160.3	125	84	6.5	20.9	11.8	3.6
	Petén Itzá	PI10	30	26.5	5.3	8.5	539	13.0	160.3	125	84	6.5	20.9	11.8	3.6
	Petén Itzá	PI11	40	26.2	3.1	8.5	548	12.9	160.6	134	85	6.7	20.8	10.9	3.5
	Petén Itzá	PI24	50	26.0	3.4	8.4	547	12.9	158.7	128	81	6.8	21.0	12.8	3.7
	Petén Itzá	PI12	60	25.9	3.7	8.4	546	12.9	156.8	123	76	6.8	21.2	14.6	3.9
	Petén Itzá	PI13	80	25.7	1.7	8.4	544	12.9	157.9	121	68	6.7	21.0	13.0	3.7
	Petén Itzá	PI15	100	25.7	3.4	8.3	543	12.9	161.6	120	81	6.5	21.2	13.8	3.1
	Petén Itzá	PI16	120	25.6	2.0	8.3	544	12.9	158.9	118	85	6.1	26.1	10.8	3.0
	Petén Itzá	PI17	140	26.1	2.0	8.2	541	12.9	157.3	125	75	4.0	19.5	6.8	3.1
	Petén Itzá	PI2	160	25.8	1.5	8.1	544	12.9	157.4	121	65	3.7	19.3	7.9	3.0
	Petexbatún	PET1	0.5	30.9	9.7	8.0	568	nd	nd	293	74	0.0	40.2	4.9	-2.9
	Petexbatún	PET5	5	30.9	9.7	8.0	568	nd	nd	354	166	0.0	48.1	5.6	-3.5
	Petexbatún	PET2	40	30.9	6.0	11.3	1 225	nd	nd	409	179	0.0	47.1	6.8	-3.8
	Salpetén	SAL1	0.5	29.7	8.4	8.2	4 310	nd	nd	122	801	0.0	351.1	142.1	4.6
	Salpetén	SAL4	15	25.6	1.6	7.5	4 290	nd	nd	171	893	0.0	410.0	156.8	4.6
	Salpetén	SAL2	37.5	25.4	0.8	7.3	4 250	nd	nd	140	796	0.0	360.7	148.2	4.7
	Ixlú river	IXL1	0.5	25.9	6.7	7.5	1 025	nd	nd	433	238	0.0	59.8	64.4	-3.9
	Perdida	PER1	0.5	28.8	9.8	8.8	232	4.2	15.1	131	43	3.8	2.2	2.7	0.4
	Perdida	PER2	4.3	26.0	7.8	8.6	234	4.2	14.9	123	35	1.9	2.1	4.8	0.6

standardized using standard deviations. The PCA suggested a correlation between conductivity and Ca^{+2}, Na^+, Mg^{+2}; between lake temperature and minimum air temperature of the coldest month, $\delta^{18}O$; between annual precipitation and precipitation of the wettest quarter, precipitation of the driest quarter; and between K^+ and ions Cl^-, SO_4^{-2}. According to the PCA, conductivity, minimum air temperature of the coldest month, maximum air temperature of the warmest month, annual precipitation, HCO_3^-, pH, and related ions Cl^-, SO_4^{-2} and K^+ were the most variable environmental attributes of the study region and were therefore selected them for further analyses to avoid undesirable effects of highly correlated variables.

A CCA (Fig. 2) (Legendre & Legendre, 2003) was performed to determine the environmental variable(s) that best explain ostracode

distribution across the karst altitudinal gradient. Analysis used 51 sediment samples, 24 study waterbodies, and all species (n = 18). We did not include the sediment samples from Lakes Amarillo (n = 1), Lacandón (n = 2) (mid-altitude), and San Diego (n = 2) (lowlands), where ostracodes were absent. The most significant environmental variables identified by the PCA (maximum air temperature of warmest month, minimum air temperature of the coldest month, conductivity, pH, precipitation, HCO_3^- and other ions [K^+, SO_4^{-2}, Cl^-]) were also included. We also considered the spatial effect (i.e. latitude, longitude and altitude) in the analysis. It, however, was a co-variable of other environmental variables presented here, so is not shown in the graphs. The behavior of the species across environmental gradients was described using locally weighted scatterplot
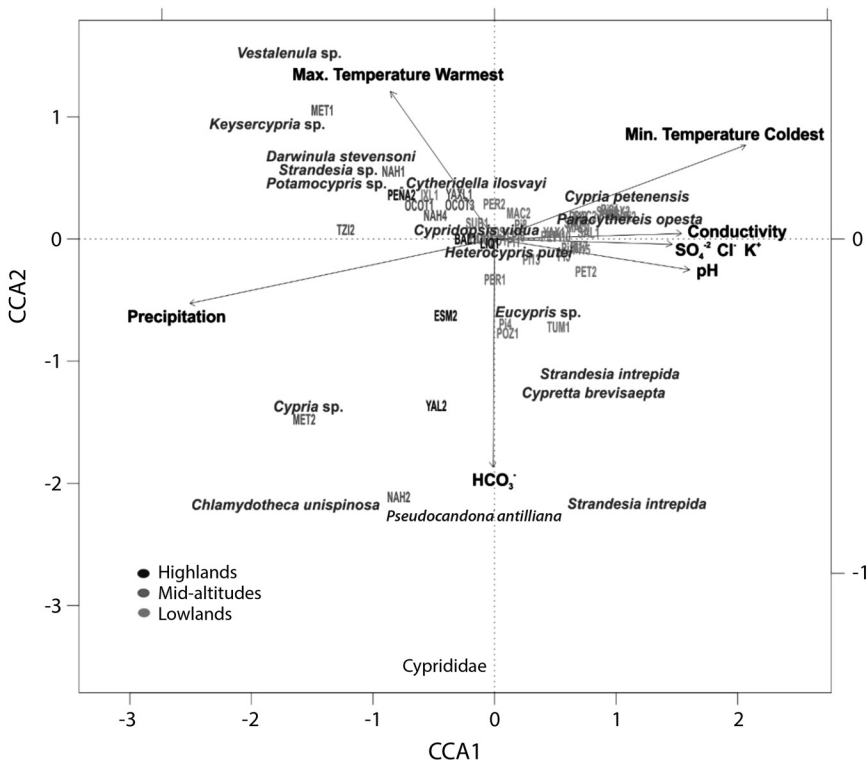

Fig. 2. Canonical Correspondence Analysis (CCA). The figure shows site ordination based on the ostracode species (in italics) and environmental variables (maximum and minimum air temperature of the warmest and coldest month, conductivity, water chemistry (K^+, SO_4^{-2}, Cl^-), pH, HCO_3^-, and annual precipitation. Arrows represent the most significant environmental variables identified previously by the PCA (Fig. 3A).
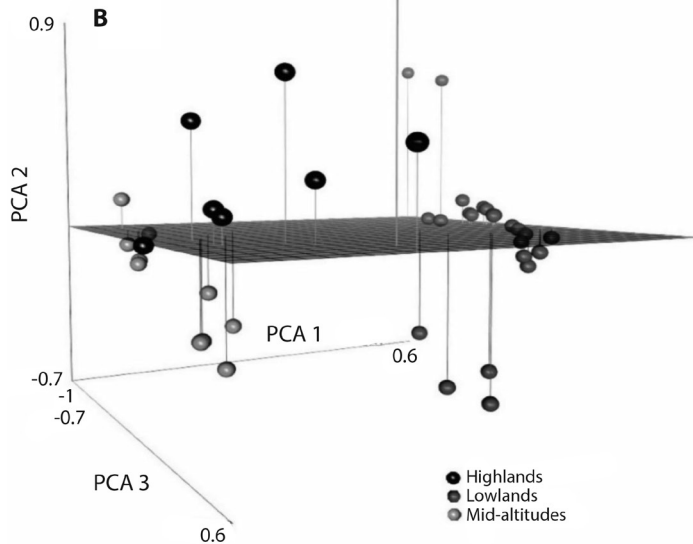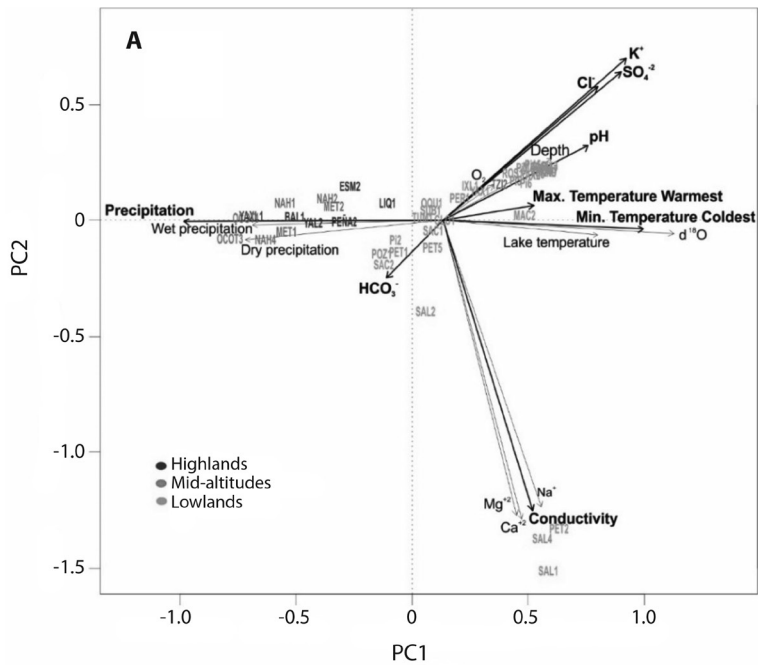
Fig. 3A. Principal Component Analysis (PCA) using limnological and regional environmental variables. The figure shows site ordination based on 13 limnological variables (water lake temperature, dissolved oxygen, pH, conductivity, water depth, $\delta^{18}O$, Ca^{+2}, K^+, Mg^{+2}, Na^+, SO_4^{-2}, Cl^-, HCO_3^-) and 5 regional environmental variables (maximum air temperature of the warmest month, minimum air temperature of the coldest month, annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter) extracted from the climate data base WorldClim. Arrows and names in black represent the most significant environmental variables identified for further analysis. For species IDs and full names see Table 3. **3B.** Principal Component Analysis sample scores for studied lakes. Sites are color coded by regional provenance (black: Montebello [coldest], dark gray: El Petén [warmest], and light gray: Lacandón forest [intermediate temperature]).

smoothing (non-parametric LOESS regression) (Correa-Metrio, Bush, Pérez, Schwalb, & Carera, 2011). Only species distributed along the whole altitude range were considered *Darwinula stevensoni* (Brady & Robertson, 1870), *Pseudocandona antilliana* Broodbakker, 1983*, Cytheridella ilosvayi* Daday, 1905 and, *Cypridopsis vidua* (O.F. Müller, 1776). All the analyses were performed using the Project R software (R Core Team, 2013) and CorelDraw X7 (Golden Software Inc., 2012).

RESULTS

Karst aquatic ecosystems across an altitude gradient in Mexico and Guatemala: Table 1 and Table 2 displays values for all limnological and regional environmental variables determined for each lake and sampling site. Surface water temperatures ranged from 21.2 °C (Yalalush) to 30.5 °C (Metzabok) and 31.4 °C (Oquevix), and dissolved oxygen from 4.1 (Metzabok and Yalalush) to 8.6 mg/l (Liquidambar). The highest value was 9.8 mg/l in Lake Perdida. Generally, shallow lakes displayed warmest waters. Stable oxygen isotope values ($\delta^{18}O$) in waters ranged from -10.06 ‰ (Liquidambar) to -2.69 ‰ (Ocotalito), to 5.6 (Oquevix pond). Studied lakes had neutral pH values, near 7 (Amarillo, Peñasquito and El Rosario), to alkaline values of about 9.4 (Oquevix pond). Conductivity values of the lake waters displayed a range from 168 µS/cm (Oquevix pond) to 4 310 µS/cm (Salpetén). Elsewhere, 246 µS/cm (Lacandón) and 712 µS/cm (Balantetic) were the minimum and maximum conductivity values for mid-altitude and highland lakes, respectively. Sulfate was highest in Lake Balantetic (137 mg/l) and Lake Macanché (242 mg/l), magnesium concentration was highest in Nahá (30 mg/l), and bicarbonate was highest also in Balantetic (285 mg/l). Lake Balantetic also displayed the highest concentration of chloride (12.1 mg/l), potassium (4.5 mg/l), and sodium (14.7 mg/l), which explains its overall high conductivity. In the lowlands of El Petén, highest individual ion concentrations were as follow: magnesium

(351 mg/l) in Lake Salpetén, bicarbonate (470 mg/l) in Lake El Rosario, chloride (42 mg/l) in Lake Macanché, potassium (7.6 mg/l) in Lake Petén Itzá, and sodium (142 mg/l) in Lake Salpetén. In general, the highland lakes of Montebello were characterized by higher sulfate concentrations, compared to the mid-elevation lakes. Lowland lakes from El Petén, Northern Guatemala, also display higher sulfate concentrations and generally higher conductivities than lakes at higher elevations.

Species richness, diversity and distribution across environmental gradients in karst Southern Mexico and Guatemala: A total of 18 ostracode species were identified in this study (Table 3; Appendix 2, Appendix 3). Most species are nektobenthic and only five are benthic. Undetermined specimens from the family Cyprididae (Baird, 1845) were restricted to the highland of Montebello. Because only valves (juveniles A-8, A-7) were found, we did not attempt to infer its ecological preferences. Table 4 displays ostracode species frequency and richness (S) for each lake. Lakes with the highest species richness were Yalalush, Peñasquito, and Esmeralda (S = 5, highlands), Nahá (S = 11, mid-altitude) and Macanché, El Rosario, Petén Itzá, and Petexbatún (S = 8, lowlands). Generally, higher S values were reported from mid-elevation. Ostracodes were absent in Lakes Amarillo and Lacandón (mid-altitude), and San Diego (lowlands). One ostracode species was found in only a single lake: *Eucypris* sp. (El Rosario, lowlands lake). Four widely distributed species were: *Darwinula stevensoni* (Brady & Robertson, 1870), *Pseudocandona antilliana* Broodbakker, 1983*, Cytheridella ilosvayi* Daday, 1905, and *Cypridopsis vidua* (O.F. Müller, 1776). Frequently encountered species included *Cypria petenensis* (Ferguson et al., 1964) (7 lakes), *Heterocypris putei* Furtos, 1936 (8 lakes), *Paracythereis opesta* (Brehm, 1939) (8 lakes), *D. stevensoni* (14 lakes), *P. antilliana* (15 lakes), *C. ilosvayi* (16 lakes), and *C. vidua* (21 lakes). *Cypria petenensis*, *H. putei* and *P. opesta* are characteristic species from the lowlands of El Petén

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TABLE 3

Ostracode species frequencies (occurrence) and richness (S) in the study lakes

	Ostracode species	EUC	CUN	CBR	VES	CPD	POT	CYA	SMA	STR	SIN	KEY	CPE	HPU	POP	DST	PAN	CIL	CVI	S
Highlands	Yalalush					x						x					x	x	x	5
	Peñasquito											x				x	x	x	x	5
	Esmeralda					x										x	x	x	x	5
	Balantetic											x				x	x		x	4
	Liquidambar																		x	1
Mid-altitudes	Nahá		x		x		x	x		x		x		x		x	x	x	x	11
	Metzabok				x			x		x		x				x	x	x	x	8
	Ocotalito						x									x	x	x		4
	T'zi BaNá							x				x						x	x	4
	Yax-há																	x		1
	Amarillo																			0
	Lacandón																			0
Lowlands*	Macanché			x							x		x		x	x	x	x	x	8
	El Rosario	x					x						x	x		x	x	x	x	8
	Petén Itzá										x		x	x	x	x	x	x	x	8
	Petexbatún										x		x	x	x	x	x	x	x	8
	Salpetén										x		x	x	x		x	x	x	7
	Sacpuy												x	x	x	x		x	x	6
	Perdida													x	x	x	x	x	x	6
	Yaxhá												x		x		x	x	x	5
	Oquevix pond			x					x	x				x				x	x	4

TABLE 3 (Continued)

Ostracode species	EUC	CUN	CBR	VES	CPD	POT	CYA	SMA	STR	SIN	KEY	CPE	HPU	POP	DST	PAN	CIL	CVI	S
Subín river		x						x		x								x	4
Las pozas														x			x	x	3
Ixlú river					x										x			x	3
Oquevix																		x	1
La Gloria																		x	1
San Diego																			0
Species frequency	1	2	2	2	2	3	3	3	3	4	6	7	8	8	14	15	16	21	

Species are ordered from lower to higher frequencies (left to right). A species frequency (bottom row) equal to 1 means that species is restricted to a single lake, whereas high frequency values indicate that the species is widely distributed. Species richness (right column) indicates the number of species in each lake. Benthic species are highlighted in gray, whereas the rest are nektobenthic tax. Information from Pérez et al. (2010, 2011). *Chlamydotheca unispinosa* (CUN), *Cypretta brevisaepta* (CBR), *Cypria petenensis* (CPE), *Cypria* sp. (CYA), Cyprididae* (CPD), *Cypridopsis vidua* (CVI), *Cytheridella ilosvayi* (CIL), *Darwinula stevensoni* (DST), *Eucypris* sp. (EUC), *Heterocypris putei* (HPU), *Keysercypria* sp. (KEY), *Paracythereis opesta* (POP), *Potamocypris* sp. (POT), *Pseudocandona antilliana* (PAN), *Stenocypris major* (SMA), *Strandesia intrepida* (SIN), *Strandesia* sp. (STR), *Vestalenula* sp. (VES).

TABLE 4
Ostracode abundance (valves 5 cm³ wet sediment) and diversity index (H) for each study lake

	Highlands					Mid-altitudes											Lowlands							
	YAL	PEÑA	ESM	LIQ	BAL	YAX	LOCOT	NAH	MET	XIB	YAX	MAC	OQU	TUM	POZ	SUB	GLO	SAC	ROS	PI	PET	SAL	IXL	PER
Taxa_S	5	5	5	1	4	1	4	11	8	4	5	8	1	3	3	4	1	6	8	8	8	7	3	6
Individuals	47	43	42	1	43	4	24	2 633	1 171	352	115	395	7	4.09	3	2	17	64	444	3 806	59	1 961	6.18	51
Dominance_D	0.3	0.4	0.3	1.0	0.7	1.0	0.4	0.2	0.3	0.4	0.8	0.4	1.0	0.5	0.3	0.5	1.0	0.3	0.3	0.3	0.3	0.6	0.5	0.4
Shannon_H	1.4	1.3	1.5	0.0	0.6	0.0	1.1	1.9	1.5	1.1	0.5	1.2	0.0	0.8	1.1	0.8	0.0	1.5	1.5	1.5	1.5	0.9	0.7	1.3
Biological diversity (e^{H}/S)	0.8	0.7	0.9	1.0	0.5	1.0	0.7	0.6	0.5	0.7	0.3	0.4	1.0	0.7	1.0	0.5	1.0	0.7	0.5	0.5	0.5	0.3	0.7	0.6
H average			0.94								1.09										0.94			

The greater the difference between e^{H} and S, the less diverse the community.

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(Pérez, 2010) and the mid-elevation lake of Nahá, Lacandón forest, however abundances are substantially higher in the lowlands. *Cypria* sp., and *Vestalenula* sp. are restricted to the mid-altitude lakes of the Lacandón forest. Finally, unidentified specimens from the family Cyprididae (Baird, 1845) were found in the upland lakes of Montebello. Greatest species diversity (H) was found in the Lacandón forest. Lake Nahá (H = 1.9), followed in diversity (H = 1.5) by highland lake Esmeralda, and lowland lakes Sacpuy, El Rosario, Petén Itzá, and Petexbatún (Table 4). In general, lakes from Lacandón forest were lightly more diverse ($H_{average}$ = 1.09) than those of the lowland El Petén and the Montebello highlands ($H_{average}$ = 0.94).

Relationship between ostracode abundance and environmental variables: The PCA was used to identify correlations between environmental variables (Fig. 3A). The first and second components explained 54 % of the total data variance. The first component (33 % of the original variance) was apparently associated with temperature and precipitation. The second component (21 % of the original variance) was apparently associated with conductivity and related ions. This analysis revealed that annual precipitation, water chemistry (SO_4^{-2}, Cl^-, and K^+), maximum and minimum air temperature of the warmest and coldest month, respectively, and conductivity, represent the widest environmental gradients along El Petén, the Lacandón forest and Montebello. Studied lakes were ordered across a well-defined temperature gradient (Fig. 3B), with the warmest sites (highest scores on Axis 1) corresponding to El Petén, Northern Guatemala. Sites with intermediate temperatures included those from the Lacandón forest, and Montebello displayed the coldest temperatures, with the lowest scores on Axis 1.

The CCA (Fig. 2) showed that minimum air temperature of the coldest month, conductivity, related ions (Cl^-, SO_4^{-2} and K^+), pH, and precipitation are the variables that best explain ostracode distributions in the study area (Axis 1), followed by maximum air temperature of

the warmest month, and HCO_3^- (Axis 2). The Lacandón forest and Montebello lakes were mostly located in the upper left positive quadrant and the warmer sites (lowlands) appear in the right quadrants. Most lowland sites displayed higher conductivities and minimum air temperatures of 17 to 18 °C. The total explained variability was 48 % and the explained variance of Axis 1 and 2 was of 42 % (species) and 92 % (environmental variables). This analysis also revealed that there are ostracodes indicative of warmer temperatures (*C. petenensis, P. opesta, Cypridopsis vidua, Eucypris* sp., *Strandesia intrepida* Furtos, 1936*,* and *Cypretta brevisaepta* Furtos, 1934). Species associated with mid-temperatures (Lacandón forest) are *Cypria* sp., *Chlamydotheca unispinosa* (Baird, 1862), *Pseudocandona antilliana* Broodbakker, 1983, *Vestalenula* sp., *Keysercypria* sp., *Darwinula stevensoni* (Brady & Robertson, 1870), *Strandesia* sp., and *Potamocypris* sp.

LOESS regressions were used to explore the response of species to the most significant environmental variables (Fig. 4), which included maximum air temperature of the warmest month, minimum air temperature of the coldest month, conductivity, HCO_3^-, annual precipitation, and pH, the four most frequent (number of lakes with the species) and widely distributed (geographically widespread) ostracode taxa were considered for these regressions (*D. stevensoni, C. viuda, Cytheridella ilosvayi* and *P. antilliana*). Analysis revealed that temperature preference was similar among two species. *C. ilosvayi,* and *P. antilliana* displayed higher abundances in temperatures ranges, from 31 to 33 °C, and tolerated coldest temperature from 12 to 18 °C, whereas, *C. vidua* is more abundant in warmer temperatures. Results for conductivity show that *P. antilliana* was found in sites with lower conductivity values (< 1 000 µS/cm) and *C. ilosvayi* displays higher abundance when conductivities exceed 2 000 µS/cm. *Cypridopsis vidua* abundances increase with conductivity, whereas *D. stevensoni* inhabits a wider conductivity range and also tolerated wider HCO_3^- values (100 to 400 mg/l), as did *C. ilosvayi*. *P. antilliana* was more

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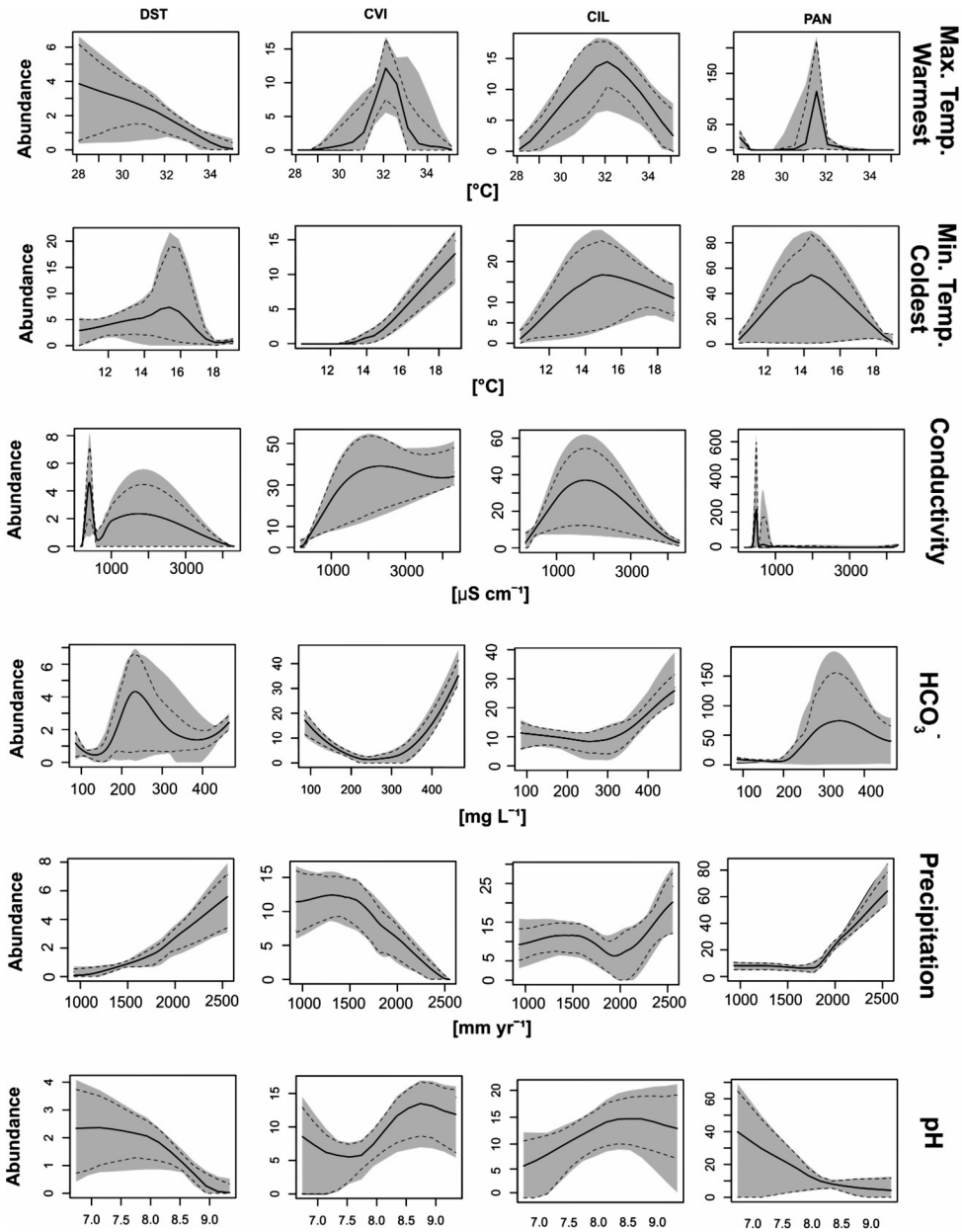
Fig. 4. LOESS regressions. Based on the PCA analysis (Fig. 3A) ostracode response to the maximum air temperature of the warmest month, minimum air temperature of the coldest month, conductivity, HCO$_3^-$, precipitation, and pH. The mean of the species response is shown as a solid black line. The gray area shows the dispersal species response between 0.025 and 0.975 validation (black dashed lines). For species IDs and full names see Table 3. The species represented here are those found along the entire altitudinal gradient (Table 4).

abundant at 300 mg/l. *Darwinula stevensoni* and *P. antilliana* were more abundant at mid-altitudes with precipitation values between 2 000 and 2 500 mm/yr. Moreover, the analysis showed that *C. ilosvayi* and *C. vidua* are the most tolerant species and are found in lakes where precipitation ranges from 1 000 to 2 500 mm/yr. With reference to the pH, *D. stevensoni* displays higher abundance at pH 7-8, whereas *P. antilliana* is indicative of pH = 7. *Cytheridella ilosvayi* and *C. vidua* are present in a wider pH range, from 7 to 9.

DISCUSSION

Karst aquatic ecosystems from El Petén, Guatemala, the Lacandón forest and Montebello, Mexico: Even though all our study lakes lie in karst terrain, they displayed large differences in morphology, maximum depth and surface temperature, determining many of its limnological characteristics (Table 1). As expected in this karst environment, all lake waters displayed high concentrations of bicarbonate, calcium, magnesium, and sulfate, and neutral to alkaline pH (Cohuo et al., 2016). The increase of bicarbonate is associated with a decrease of the allochthonous silicate fraction (Battistel et al., 2018). It is reasonable that the higher rainfall during the wet season favor the transport of silicate material into the lake, while higher lake levels dilute carbonates and prevent their precipitation. The higher ionic strength observed in the lowlands could be explained by higher evaporation rates and surface temperatures (Pérez et al., 2013), but may also reflect localized deposits of evaporite minerals in some El Petén watersheds. Temperatures and stable isotope values in lake surface waters are probably explained by the altitude gradient. It is well known that lower $\delta^{18}O$ values suggest higher lake levels (Rosenmeier et al., 2002), explain by a negative balance between evaporation (E) and precipitation (P) (Curtis, Brenner, & Hodell, 1998). Disparities in E/P at different altitudes explain the limnological differences between lakes of the El Petén lowlands, the mid-elevation Lacandón forest

and the Montebello highlands. This is illustrated by comparing the stable isotope values of lake waters from these three areas, with more negative values at higher elevations (Table 2). The highest values shown by Lake Balantetic, Montebello, with respect to conductivity, chloride, calcium, potassium, and sodium, can be explain because this lake has been classified as an *uvala* (Alcocer et al., 2016). *Uvalas* typically display elliptical, i.e. elongate shapes, as they are formed by two or more coalesced dolines. Lake Balantetic lowest mean width (0.23 km), depth (< 3 m), and small superficial area (13.6 ha) (Alcocer et al., 2016) has an important effect on determinate the chemical parameters, as well as the movement of water within the lake, and the sedimentary inputs from the drainage basin (Wetzel, 2001).

Ostracodes diversity across an altitudinal gradient: The ostracode fauna of the study area reflects the limnological heterogeneity of the region, displaying different distributional patterns and ecological preferences. *Cypridopsis vidua* (O.F. Müller, 1776), *Cytheridella ilosvayi* Daday, 1905, *Pseudocandona antilliana* Broodbakker, 1983, and the cosmopolitan species *Darwinula stevensoni* (Brady & Robertson, 1870; Cohuo et al., 2016; D' Ambrosio, García, Díaz, Chivas, & Claps, 2017) are the most tolerant species and are distributed across the entire altitudinal gradient (Table 4). They show great morphological variability, which may allow them to adapt to a wide range of environmental conditions (Gandolfi, Benedetta, Van Doninck, Rossi, & Menozzi, 2009; Cohuo et al., 2016). The identification of tolerance species, are important for paleoecological investigations, because they can serve as modern analogues for reconstructing the Quaternary history of the area. The great abundance of *Cypria petenensis* (Ferguson *et al*., 1964), *Heterocypris putei* Furtos, 1936 and *Paracythereis opesta* (Brehm, 1939) in the lowlands can be associated to habitats with higher surface water temperatures, primarily in littoral zones with abundant macrophytes (Pérez et al., 2012). Thus, seems to be a good indicators of low lake

levels (< 40 m). Although there is evidence that *C. petenensis* is a species able to tolerate deeper waters (< 60 m). Specifically, *H. putei* is known to be distributed in Yucatán Peninsula, Mexico, Northern Guatemala, and Belize (Cohuo et al., 2016). Moreover, *P. opesta* has been reported as a thermocline indicator (Pérez et al., 2012). Finally, *C. petenensis* as well as *P. opesta* have been reported in Central Southern Yucatán Peninsula and Belize (Cohuo et al., 2016). Our data demonstrate that the mid-elevation lakes are more diverse (Table 4), suggesting that this region has a high potential for harboring microrefugia. This is due the intersection of two biogeographic zones across steep environmental gradients, where Neotropical taxa from Central America and the Yucatan Peninsula intermingle with Nearctic elements from Central Mexico (Bush, 2002; Correa-Metrio, Meave, Lozano-García, & Bush, 2014; Franco-Gaviria et al., 2018). In contrast, the low diversity found in Montebello highlands, may be explained by the higher altitude, lower temperature, and higher erosion, as well as variables we did not consider, such as abundance of aquatic macrophytes, contamination, predation by fish and invertebrates, among other factors (Pérez, 2010; Olea-Olea & Escolero, 2015). The most plausible explanations for the lack of ostracodes in Lakes Amarillo and Lacandón (mid-altitude), and San Diego (lowlands) is 1) a structural difference of habitats, where there are zones with a more homogeneous habitat and less resources of food (Hernández, Escobar, & Alcocer, 2010); 2) a high abundance of Cladocera, a taxon that has been observed as competitor for ostracodes (Umaña-Villalobos, Avilés-Vargas, & Esquivel-Garrote, 2018).

Ostracodes ecology - temperature, conductivity, and precipitation indicators: These gradients are most likely associated with the steep altitudinal gradient of the region (Fig. 3A, Fig. 3B). Thus, it was expected that the ostracodes fauna would respond to these variables, an observation confirmed by the CCA (Fig. 2). The distribution of samples along the first three axes of the PCA (Fig. 3B) suggests that air temperature plays an important role in structuring the regional environmental gradients. Previous studies focused on the lowlands reported that conductivity and water depth were the main controlling variables in that environment (Pérez, 2010; Pérez et al., 2013). Our examination across this altitude gradient revealed that additional variables are important influences on tropical ostracodes. Precipitation and altitude are directly related in the study area (Fig. 1) (Pérez et al., 2010) and data analyses showed that precipitation is one of the most important variables controlling ostracodes, influencing inversely pH and conductivity. The hydrologic balance in areas across Mexico is described by the relative amount of evaporation (E) to precipitation (P). The Mexican deserts, the inner Northern basin and most of the Yucatán Peninsula lowlands display a negative moisture balance, that is E > P (Pérez, 2010). The different moisture balances across this latitudinal gradient explain the differences observed in the lakes and therefore the presence/absence of ostracodes species. It might be assumed that temperature would not be an important variable in the tropics because differences between lowland and highland sites are relatively small. For instance, Pérez et al. (2011) reported in the lowlands surface water temperatures from 21.6 to 32.0 °C (range = 10.4 °C), which is small relative to water temperature ranges compared with higher latitudes. Nevertheless, ostracodes development depends on water temperature (Mezquita, Roca, & Wansard, 1999; Smith & Delorme, 2010), our results suggest that maximum and minimum air temperature of the warmest and coldest month are a factor that influences ostracodes distribution and abundance in the study area. The inclusion of the air temperature allows to cover all the temporality in which the species develop. For example, the distribution of species from the Northern hemisphere may be limited in its Southern extension by the highest average temperatures in July (summer) that adults can tolerate, but its extension to the north could be more influenced by minimum winter temperatures (January) in which eggs at rest can survive

(Horne, 2008). This approach can be a solution to avoid seasonal sampling, where access to the research areas are difficult and resources are limited. It has been demonstrated that species occurrences can be defined usefully in terms of the geographical distribution of mean July and January air temperature ranges. Therefore, using the WorldClim data set to calibrate species' temperature ranges might facilitate an estimation of past air temperatures (Horne, 2007), allowing thus more detailed paleoclimate reconstructions.

LOESS regressions yielded species ecological information for the benthic *Darwinula stevensoni, Cytheridella ilosvayi, Pseudocandona antilliana* and nektobenthic *Cypridopsis viuda.* Due to *D. stevensoni* has a cosmopolitan distribution, this has been shown to be a highly tolerant specie (Cohuo et al., 2016). Regardless of their life stage or type of habitat, showed high survival values even in extreme conditions (D' Ambrosio et al., 2017). Different studies indicated higher abundances in sites with precipitation from 2 000 to 2 500 mm/yr, a broad range of conductivities, and temperatures less than 32 °C (Gandolfi et al., 2009). Our results suggest an association more to cooler temperatures (28 ºC) and lower conductivities (1 500 mm/yr), which contributes to reinforce its high tolerance range estimated globally. *Cytheridella ilosvayi* displays a wider precipitation and conductivity range (1 000-2 500 mm/yr and 1 000-3 000 µS/cm, respectively). This specie also tolerates high temperatures values (32 °C). Our results allow us to confirm previous observations that show that this specie is an indicator of warm and humid conditions (Pérez et al., 2012). As for *P. antilliana* shows a preference for sites with higher precipitation (2 000-2 500 mm/yr), lower conductivity (< 1 000 µS/cm) and lower temperatures (14 °C). Therefore, it is possible to consider this specie as an indicator of cold and humid conditions. Finally*, C. vidua,* regression analysis suggests that is most abundant when precipitation ranges from 1 000 to 1 500 mm/yr, and declines with higher rainfall values, conductivity and HCO_3^- relatively high (most abundant at 2 000 µS/cm

and 400 mg/l, respectively), and temperature range from 31 to 33 °C. *Cypridopsis vidua* seems to be more associated with warm, low-rainfall environments, such as recorded in the lowlands of Guatemala. However, *C. viuda* is found in low numbers during summer months in Argentina, where salinity is < 29g/l (D' Ambrosio et al., 2017). Although these environmental conditions are important for this species, it has been reported that abundant aquatic plants are crucial for its development, since it is a nektobenthic specie, and it can therefore be used as a paleobioindicator of vegetated littoral zones (Pérez, 2010; Pérez et al., 2012). Based on pH, it was expected that the species were adapted to neutral to alkaline values, due to the fact that it is a karstic environment. However, only *C. vidua* and *C. ilosvayi* shown a wider range (7-9), reflecting their high tolerance and distribution along the altitudinal region (Cohuo et al., 2016). *Darwinula stevensoni* and *P. antilla* have shown greater association to environments towards neutral values as observed in other studies (Meisch, 2000; Külköylüoğlu, 2011). Therefore, pH is an ecological variable that influence ostracodes and more studies need to explore in detail.

Due to agricultural activities, the severe contamination, rapid ecosystem fragmentation and habitat loss in the Northern Neotropical region (Olea-Olea & Escolero, 2015), it is relevant to increase the effort in study the lakes and surrounding areas. Our results highlight that 1) ostracodes distributions are explained by a combination of the environmental variables air temperature, conductivity, and precipitation; 2) we provide basic information on the state of the lakes, however detailed limnological studies, including nutrient and contaminant analyses, should be conducted in the future, as well as consider the role of variables such as substrate, aquatic plant cover and species interactions (competition, parasitism, and predation) in shaping ostracodes communities; 3) despite the idea that a seasonal sampling is necessary for a more effective use of ostracodes as proxies for environmental reconstructions, the application of environmental variables from WorldClim

data sets allows to calibrate species based on their potential to exist in any geographical location within its environmental variables range, provided that local conditions satisfy its other environmental requirements. Hence, our data showed the communities associations with the environment and might facilitate more detailed palaeoclimate reconstructions for the late Quaternary history of the area.

Declaración de ética: los autores declaran que todos están de acuerdo con esta publicación y que han hecho aportes que justifican su autoría; que no hay conflicto de interés de ningún tipo; y que han cumplido con todos los requisitos y procedimientos éticos y legales pertinentes. Todas las fuentes de financiamiento se detallan plena y claramente en la sección de agradecimientos. El respectivo documento legal firmado se encuentra en los archivos de la revista.

ACKNOWLEDGMENTS

RESUMEN

Ostrácodos neotropicales como indicadores ambientales en un gradiente altitudinal de Guatemala y México. Los ostrácodos son microcrustáceos acuáticos, que poseen un caparazón bivalvo de carbonato de calcio que se puede preservar en los sedimentos de los ambientes lacustres. Debido a su alta sensibilidad a cambios ambientales y su alta potencialidad de fosilización, los ostrácodos son una herramienta útil para el estudio paleoclimático y paleoambiental, abarcando una temporalidad de décadas hasta millones de años. El conocimiento ecológico de las especies, así como su taxonomía son prerrequisitos para estos estudios. Sin embargo, esta información es aún escasa en diferentes regiones del mundo, incluyendo el Neotrópico. Hasta el momento, se han realizado únicamente estudios en los lagos kársticos de las tierras bajas de la Península de Yucatán, en el norte del Neotrópico. Sin embargo, los lagos en altitudes medias y altas permanecen poco conocidos. El objetivo de este trabajo es aportar conocimiento de ostrácodos no-marinos neotropicales a lo largo de un gradiente altitudinal que va desde las tierras bajas de El Petén, Guatemala (100-500 m s.n.m.), incluyendo los lagos de tierras medias de la Selva Lacandona (500-1 000 m s.n.m.), hasta las tierras altas de Montebello, Chiapas, México (1 000-1 500 m s.n.m.). Dieciocho especies de ostrácodos se identificaron en 24 lagos, pero estuvieron ausentes en los lagos Amarillo y Lacandón (tierras medias) y San Diego (tierras bajas). La ausencia de ostrácodos podría explicarse por la falta de un muestreo estacional o por variables que no se consideraron en este estudio como sustrato, cobertura vegetal acuática e interacciones interespecíficas. Los análisis estadísticos indicaron que las especies más abundantes son: *Cypridopsis vidua* (O.F. Müller, 1776)*, Cytheridella ilosvayi* Daday, 1905, *Pseudocandona antilliana* Broodbakker, 1983 y *Darwinula stevensoni* (Brady & Robertson, 1870), con una distribución continua a lo largo del gradiente altitudinal. Algunas especies presentan una distribución más restringida, determinada por la temperatura, precipitación y conductividad. Por ejemplo, *Eucypris* sp. está restringida a las tierras bajas; mientras que *Vestalenula* sp. y *Cypria* sp. se encontraron únicamente en elevaciones medias. La diversidad de especies es ligeramente mayor en lagos cálidos a altitudes medias ($H_{average}$ = 1.09) que en las tierras bajas ($H_{average}$ = 0.94) y que en lagos de agua más fría en las tierras altas ($H_{average}$ = 0.94), sugiriendo que los lagos de tierras medias

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tienen un alto potencial para albergar micro-refugios. Las regresiones LOESS muestran las preferencias ecológicas de las cuatro especies más frecuentes y altamente distribuidas con respecto a la temperatura, conductividad, HCO$_3^-$, precipitación y pH. *Darwinula stevensoni* se asocia a temperaturas frías y conductividades bajas, lo que evidencia su alto rango de tolerancia. *Cypridopsis vidua* se asocia con ambientes cálidos y de baja precipitación, como los registrados en las tierras bajas de Guatemala, y puede usarse como paleobioindicador de zonas de vegetación litoral. *Cytheridella ilosvayi* es un indicador de condiciones cálidas y húmedas, mientras que *P. antilliana* de frías y húmedas. Esta información ecológica-cuantitativa se podrá utilizar como una herramienta para las reconstrucciones paleoambientales basadas en ostrácodos en el sur de México y norte de Guatemala. Además, este enfoque sirve como modelo para futuros estudios paleoecológicos que emplean otros bioindicadores acuáticos, como las amebas testadas, los cladóceros y los quironómidos.

Palabras clave: ostrácodos no marinos; diversidad; ecología; Neotrópico.

REFERENCES

Alcocer, J., Oseguera, L. A., Sánchez, G., González, C. G., Martínez, J. R., & González, R. (2016). Bathymetric and morphometric surveys of the Montebello Lakes, Chiapas. *Journal of Limnology, 75*, 56-65.

American Public Health Association (APHA), American Water Works Association (AWWA), Water Pollution Control Federation (WPCF). (1995). *Standard Methods for the Examination of Water and Wastewater*. Washington, USA: American Public Health Association.

American Public Health Association (APHA). (1998). *Standard methods for the examination of water and wastewater*. Washington, USA: American Public Health Association.

American Public Health Association (APHA), American Water Works Association (AWWA), Water Pollution Control Federation (WPCF). (2005). Standard Methods for the Examination of Water and Wastewater. Maryland, USA: American Public Health Association.

Anselmetti, F. S., Ariztegui, D., Hodell, D. A., Hillesheim, M. B., Brenner, M., Gilli, A., ... Mueller, A. D. (2006). Late Quaternary climate-induced lake level variations in Lake Petén Itzá, Guatemala, inferred from seismic stratigraphic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology, 230*(1-2), 52-69.

Armienta, M. A., Ongley, L. K., Rodríguez, R., Cruz, O., Mango, H., & Villaseñor, G. (2008). Arsenic distribution in mesquite *(Prosopis laevigata)* and huizache *(Acacia farnesiana)* in the Zimapán mining area, México. *Geochemistry Exploration, Environment, Analysis, 8*, 1-7.

Basterrechea, M. (1988). Limnología del Lago Petén Itzá, Guatemala. *Revista de Biología Tropical, 36*(1), 123-127.

Battistel, D., Roman, M., Marchetti, A., Kehrwald, N., Radeelli, M., & Balliana, E. (2018). Antropogenic impact in the Maya lowlands of Petén, Guatemala, during the last 5500 years. *Journal of Quaternary Science, 33*(2), 166-176.

Brenner, M., Rosenmeier, M., Hodell, D., & Curtis, J. (2002). Paleoclima de la región maya: síntesis del conocimiento basado en registros paleolimnológicos. *Los Investigadores de la Cultura Maya, 1*, 248-261.

Brezonik, P., & Fox, J. (1974). The limnology of selected Guatemalan lakes. *Hydrobiologia, 45*, 467-487.

Bush, M. B. (2002). Distributional change and conservation on the Andean flank: A palaeoecological perspective. *Global Ecology and Biogeography, 11*, 463-467.

Canudo, J. (2002). Ostrácodos. In E. Molina (Ed.), *Micropaleontología* (pp. 399-418). Zaragoza, España: Colección Textos Docentes.

Cohuo, S., Macario-González, L., Pérez, L., & Schwalb, A. (2016). Overview of Neotropical-Caribbean freshwater ostracode fauna (Crustacea, Ostracoda): identifying areas of endemism and assessing biogeographical affinities. *Hydrobiologia, 786*, 5-21.

Correa-Metrio, A., Bush, M. B., Pérez, L., Schwalb, A., & Carera, K. R. (2011). Pollen distribution along climatic and biogeographic gradients in northern Central America. *The Holocene, 21*(4), 681-692.

Correa-Metrio, A, Bush, M. B, Hodell, A., Brenner, M., Escobar, J., & Guilderson, T. (2012). The influence of abrupt climate change on the ice-age vegetation of the Central American lowlands. *Journal of Biogeography, 39*, 497-509.

Correa-Metrio, A., Meave, J. A., Lozano-García, S., & Bush, M. B. (2014). Environmental determinism and neutrality in vegetation at millennial time scales. *Journal of Vegetation Science, 25*, 627-635.

Curtis, J., Brenner, M., & Hodell, D. (1998). A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. *Journal of Paleolimnology, 19*, 139-159.

D' Ambrosio, D., García, A., Díaz, A., Chivas, A., & Claps, M. (2017). Distribution of ostracods in west-central Argentina related to host-water chemistry and climate: implications for paleolimnology. *Journal of Paleolimnology, 58*, 101-117.

Danielpol, D., Ito, E., Wansard, G., Kamiya, T., Cronin, T., & Baltanás, A. (2002). Techniques for collection and study of ostracoda. In J. Holmes & A. Chivas (Eds.), *The Ostracoda, applications in quaternary research* (pp. 6597). Washington, USA: American Geophysical Union.

Deevey, E. S., Brenner, M., Flannery, M. S., & Yezdani, G. H. (1980). Lakes Yaxha and Sacnab, Peten, Guatemala: limnology and hydrology. *Archiv fur Hydrobiologie, 57*(419), e460.

Díaz, K., Pérez, L., Correa-Metrio, A. Franco-Gaviria, F., Echeverría, P., Curtis, J., & Brenner, M. (2017). Holocene environmental history of tropical, mid-altitude Lake Ocotalito, México, inferred from ostracodes and non-biological indicator. *The Holocene, 27*(9), 1308-1317.

Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surface for global land areas. *International Journal of Climatology, 37*, 4302-4315.

Ford, D. C. & Williams, P. W. (2007). *Karst hydrology and geomorphology.* Londres: Wiley Chichester.

Franco-Gaviria, F., Correa-Metrio, A., Cordero-Oviedo, C., López-Pérez, M., Cárdenes-Sandí, G., & Romero, F. (2018). Effects of late Holocene climate variability and antropogenic stressors on the vegetation of the Maya highland. *Quaternary Science Reviews, 189,* 76-90.

Gandolfi, A., Benedetta, E., Van Doninck, K., Rossi, V., & Menozzi, P. (2009). Salinity tolerance of *Darwinula stevensoni* (Crustacea, Ostracoda). *Italian Journal of Zoology, 68*, 61-67.

Golden Software, Inc. (2012). *CorelDraw X7*. Corel Corporation. Ottawa, Canada. Retrieved from https://www.coreldraw.com/la/pages/coreldraw-x7

Griffiths, H., & Holmes, J. (2000). *Non-marine Ostracods and Quaternary Palaeoenvironments*. London: Quaternary Research Association.

Hernández, C., Escobar, E., & Alcocer, J. (2010). Ensamble de crustáceos bentónicos en un lago salino tropical. *Revista Mexicana de Biodiversidad, 81*, S133-S140.

Holdridge, L. R. (1975). Taller sobre mapificación ecológica en el nivel de zonas de vida. Guatemala: FAO.

Horne, D. (2007). A mutual temperature range method to Quaternary palaeoclimatic analysis using European nonmarine Ostracoda. *Quaternary Science Reviews, 26*, 1398-1415.

Horne, D. (2008). Palaeoclimatic applications of large databases: developing and testing methods of palaeotemperature reconstruction using nonmarine ostracods. *Senckenbergiana lethaea, 88*, 93-112.

Jost, L. (2006). Entropy and diversity. *Oikos, 113*, 363-375.

Kauffer, F., & Villanueva, C. (2011). Retos de la gestión de una cuenca construida: la península de Yucatán en México. *Aqua-LAC, 3*, 81-91.

Krebs, C. (1989). *Ecological Methodology.* New York: Harper and Row Publishers.

Kueny, J. A., & Day, M. J. (2002). Designation of protected karstlands in Central America: a regional assessment. *Journal of Cave and Karst Studies, 64*, 165-174.

Kutterolf, S., Schindlbeck, J. C., Anselmetti, F. S., Ariztegui, D., Brenner, M., Curtis, J., ... & Wang, K. L. (2016). A 400-ka tephrochronological framework for Central America from Lake Petén Itzá (Guatemala) sediments. *Quaternary Science Reviews, 150*, 200-220.

Külköylüoğlu, O. (2011). Ecology of freshwater Ostracoda (Crustacea) from Lakes and Reservoirs in Bolu, Turkey. *Journal of Freshwater Ecology, 18*(3), 343-347.

Legendre, P., & Legendre, L. (2003). *Numerical Ecology*. Canada: Elsevier.

Manoharan, V., Welch, R., & Lawton, R. (2009). Impact of deforestation on regional surface temperatures and moisture in the Maya lowlands of Guatemala. *Geophysical Research Letters, 36*(21), L21701.

Meisch, C. (2000). *Freshwater Ostracoda of western and central Europe*. Berlin, Germany: Spektrum Akademischer Verlag GmbH.

Mezquita, F., Roca, J. R., & Wansard, G. (1999). Moulting, survival and calcification: the effects of temperature and water chemistry on an ostracod crustacean (*Herpetocypris intermedia*) under experimental conditions. *Archiv für Hydrobiologie, 146*, 219-238.

Moreira, J., McNab, R., García, R., Córdova, F. H., Dubón, T., Córdova, M., & Soto, J. (2007). Abundancia y patrones diarios de actividades del Jabalí (*Tayassu pecari*) en la región Este del Parque Nacional Mirador-Río Azul, Petén, Guatemala. *Suiform Soundings, 7*, 31-33.

Moreno, C. E. (2010). Métodos para medir la biodiversidad. M&T-Manuales y Tesis SEA. Zaragoza, España: GORFI, S.A

O'Brien, N. R., & Pietraszek-Mattner, S. (1998). Origin of the fabric of laminated fine-grained glaciolacustrine deposits. *Journal of Sediment Research, 68*, 832-840.

Olea-Olea, S., & Escolero, O. (2015). Analysis agriculture's impact in a system of lakes on a karst environment with tropical climate. *EGU General Assembly Conference Abstracts, 17*, 7233.

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 67(4): 1037-1058, September 2019

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Pérez, L. (2010). *Non-marine ostracodes from the Yucatán Peninsula as late Quaternary paleoenvironmental indicators* (Doctoral thesis). Architektur, Bauingenieurwesen und Umweltwissenschaften, Technische Universität Braunschweig, Braunschweig, Germany.

Pérez, L., Bugja, R., Massaferro, J., Steeb, P., Van Geldern, R., Frenzel, P., ... Schwalb, A. (2010). Post-Columbian environmental history of Lago Petén Itzá, Guatemala. *Revista Mexicana de Ciencias Geológicas, 27*, 490-507.

Pérez, L., Lorenschat, J., Bugja, R., Brenner, M., Hoelzmann, P., Islebe, G., ... Schwalb, A. (2011). Aquatic ecosystems of the Yucatán Peninsula and surrounding areas. *Hydrobiologia, 661*, 407-433.

Pérez, L., Frenzel, P., Hoelzmann, P., Escobar, J., Brenner, M., Scharf, B., & Schwalb, A. (2012). Late Quaternary (24-10 ka BP) environmental history of the Neotropical lowlands inferred from ostracodes in sediments of Lago Petén Itzá, Guatemala. *Journal of Paleolimnology, 46*, 59-74.

Pérez, L., Lorenschat, J., Massaferro, J., Pailles, C., Sylvestre, F., Hollwedel, W., ... Schwalb, A. (2013). Bioindicators of climate and trophic state in lowland and highland aquatic ecosystems of the northern Neotropics. *Revista de Biología Tropical, 61*(2), 603-644.

Pielke, R. A., Davey, C. A., Niyogi, D., Souleymane, F., Steinweg-Woods, J., Hubbard, K., … Blanken, P. (2007). Unresolved issues with the assessment of multidecadal global land surface temperature trends. *Journal of Geophysical Research, 112*, D24S08. DOI: 10.1029/2006JD008229

R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Ramírez, N. (2007). *Programa de conservación y manejo Parque Nacional Lagunas de Montebello*. México: Comisión Nacional de Áreas Naturales Protegidas.

Rosenmeier, M., Hodell, D., Brenner, M., Curtis, J., Martin, J., Anselmetti, F., … Guilderson, T. (2002). Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine 18 O records. *Journal of Paleolimnology, 27*, 117-131.

Rzedowski, J. (2006). *Vegetación de México*. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Smith, A., & Delorme, L. (2010). Ostracoda. In J. Thorp & A. Covich (Eds.), *Ecology and Classification of North American Freshwater Invertebrates* (pp. 725-771). Amsterdam: Elsevier.

Umaña-Villalobos, G., Avilés-Vargas, L., & Esquivel-Garrote, O. (2018). Zooplankton variation in Fraijanes Lake (Costa Rica) during the course of one year. *Revista de Biología Tropical, 66*(1), S123-S131.

Vázquez-Molina, Y., Correa-Metrio, A., Zawisza, E., Franco-Gaviria, J. F., Pérez, L., Romero, F., … Esperón-Rodríguez, M. (2016). Decoupled lake history and regional moisture availability in the middle elevations of tropical Mexico. *Revista Mexicana de Ciencias Geológicas, 33*(3), 355-364.

Vester, H. F., Lawrencce, D., Eastman, J. R., Turner, B. L., Calmé, S., Dickson, R., … Sangermano, F. (2007). Land change in the southern Yucatán and Calakmul biosphere reserve: effects on habitat and biodiversity. *Ecological Applications, 17*(4), 989-1003.

Villanueva, M. (2011). *Selva Lacandona*. México: World Wildlife Fund.

Wetzel, R. G. (2001). *Limnology: lake and river ecosystems*. San Diego, USA: Academic Press.