UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
BIOLOGÍA EVOLUTIVA

COMUNIDADES DISPARES DE ANFIBIOS Y REPTILES DURANTE EL CUATERNARIO COMO UNA RESPUESTA A LA VEGETACIÓN EN MOSAICO Y AL CAMBIO CLIMÁTICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS
PRESENTA:
JOSÉ ALBERTO CRUZ SILVA

TUTOR(A) PRINCIPAL DE TESIS: DR. VÍCTOR HUGO REYNOSO
INSTITUTO DE BIOLOGÍA, UNAM
COMITÉ TUTOR: DRA. SOCORRO LOZANO GARCÍA
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DR. JOAQUÍN ARROYO CABRALES
INSTITUTO NACIONAL DE ANTROPOLOGÍA E HISTORIA

MÉXICO, Cd. Mx. MARZO, 2017

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UNAM POSGRADO
Ciencias Biológicas

COORDINACIÓN

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 7 de noviembre de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **CRUZ SILVA JOSÉ ALBERTO** con número de cuenta **510007568** con la tesis titulada: **"Comunidades dispares de anfibios y reptiles durante el Cuaternario como una respuesta a la vegetación en mosaico y al cambio climático"**, realizada bajo la dirección del **DR. VÍCTOR HUGO REYNOSO ROSALES:**

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Suplente	DR. JOAQUÍN ARROYO CABRALES

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 13 de febrero de 2017.

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

c.c.p. Expediente del (la) interesado (a).

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CUADRO DE CONTENIDOS

RESUMEN

La destrucción del hábitat, el cambio de uso de suelo, la contaminación, la introducción de especies invasoras y el calentamiento global están alterando actualmente la diversidad del planeta. El uso de la paleobiología o paleoecología para conocer cómo funcionan las comunidades actuales frente a cambios ambientales y climáticos ha tomado un auge importante en los últimos años. Los microvértebrados han mostrado características importantes para utilizarlos como proxies para la reconstrucción de ambientes y climas pasados. Los anfibios y reptiles pleistocénicos han sido poco estudiados en México y Centroamérica comparado con Europa y Norteamérica y los estudios paleomastozoológicos en México; por lo que el uso de la herpetofauna para reconstruir paleoclimas y paleoambientes no ha sido utilizado en México. Los microvertebrados no alteran de manera sustancial los ambientes como lo hizo la megafauna en el pasado formando comunidades vegetales no análogas con el presente. Esto permite que se pueda estudiar la estructura de las comunidades de vertebrados pequeños, a través del tiempo, como respuesta a lo cambios ambientales y climáticos. Estudiando los anfibios y reptiles pleistocénicos de la Gruta de Loltún en Yucatán, la Cueva de San Josecito en Nuevo León y el Desierto Sonorense, en México, se infirió el paleoclima de cada uno de los sitios por medio del método de *mutual climatic range* (intervalo climático mutuo). El paleoambiente se infirió por medio del método de ponderación de hábitat y se comparó la estructura de las comunidades de anfibios y reptiles fósiles con las del Presente, para observar cambios en la estructura de la vegetación y cambios en la distribución de las especies.

En todos los sitios estudiados se encontraron comunidades de anfibios y reptiles pleistocénicas no análogas con el presente. Comunidades dispares de herpetofauna

concuerdan con el cambio de la estructura de vegetación en mosaico, durante el Pleistoceno, a franjas durante el Holoceno. Esto propició la extirpación de algunos taxa en ciertos sitios (Capítulo I, II, IV) o la extinción de especies (Capítulo III), contrario a lo que maneja al Hipótesis de Estabilidad Herpetológica durante el Cuaternario propuesta en los 90. La inferencia paleoclimática y paleoambiental utilizando anfibios y reptiles es confiable, ya que se asemeja a las reconstrucciones paleoambientales y paleoclimáticas obtenidas con otros proxies como el polen, diatomeas, registros glaciares, sedimentos, isótopos, etc., en los mismos sitios o en sitios cercanos. La estructura de las comunidades de anfibios y reptiles responde a ambos factores, estructura de la vegetación (ambiental) y el clima, pero el saber cuál de los dos es más importante queda sin resolverse. Finalmente, se propone un método alternativo para reconstruir paleoclimas con vertebrados utilizando la relación abundancia con el centroide del nicho climático (Capítulo V). En caso de no tener un sitio con buena representación fósil a nivel comunidad, se puede utilizar la abundancia de un taxón, ya que las características demográficas son las primeras en verse afectadas durante eventos de cambios ambientales y climáticos.

ABSTRACT

The main factors that affect biodiversity are habitat loss, land use change, pollution, introduction of exotic species and climate change. In recent years, the use of paleobiology or paleoecology to study how current communities respond to environmental and climatic changes has been of great importance. Small vertebrates have important characteristics that let us use them as proxies for the reconstruction of past climates and environments. In Mexico and Central America, pleistocene amphibians and reptiles have been poorly studied. Unlike the megafauna in the past, which used to form vegetation communities not analog to the present ones, small vertebrates do not affect or influence vegetation structure and composition. Therefore, this allows that small vertebrates community structure can be studied, through time, as a response to climate and environmental changes including vegetation. We studied pleistocene amphibians and reptiles in Loltún Cave, Yucatán, San Josecito Cave in Nuevo León and in the Sonoran Desert, Mexico, to infer the paleoclimate in each site using the mutual climatic range method. Paleoenvironment was inferred with the habitat weighting method. To observe changes in vegetation structure and in species distribution, the community structure of fossil amphibians and reptiles was compared with the current ones.

In the three sites that were studied, we found that the amphibians and reptiles communities are not analog with present ones. Disparity communities of herpetofauna are in accordance with the changes in vegetation structure from mosaic during the Pleistocene to striped vegetation in the Holocene. This caused the loss of some taxa in the sites (Chapters I, II, IV) and the extinction of some species (Chapter III), conversely to what is stated in the Quaternary Herpetofaunal Stability Hypothesis. Paleoclimatic and paleoenvironmental

inferences using amphibians and reptiles are reliable. They resemble the paleoenvironments and paleoclimates obtained in the same sites using other proxies such as pollen, diatoms, glacial records, sediments and isotopes, among others. Amphibians and reptiles community structure responds to both factors: vegetation structure (environmental) and climate, being both equally important. Finally, we propose a new method with small vertebrates, it consists in using the relationship between abundance and climatic niche centroid (Chapter V) for paleoclimatic reconstructions. Since demographic characteristics are the first ones to be affected during climatic and environmental changes, this method allows the use of the taxon abundance when the fossil record does not reflect the community structure.

INTRODUCCIÓN GENERAL

El ser humano actualmente es el factor principal de disturbio de la biota (Dietl *et al.*, 2016). La destrucción del hábitat, el cambio de uso de suelo, la contaminación, la introducción de especies invasoras y el cambio climático están alterando actualmente la diversidad del planeta (Birks *et al.*, 2016). El conocer cómo reaccionarán las comunidades ante los factores de cambio antropogénico se ha hecho una prioridad para la conservación de la biodiversidad (Kerr *et al.* 2013; Titeux *et al.*, 2016); sin embargo, el futuro está lleno de incertidumbre (Kerr *et al.*, 2013). El uso de la paleobiología o paleoecología para conocer cómo funcionan las comunidades actuales frente a cambios ambientales y climáticos ha tomado un auge importante en los últimos años (Louys 2012; Dietl *et al*, 2015; Dietl 2016) para inferir como reaccionarán las especies a cambios ambientales futuros (Birks *et al.*, 2016).

La paleobiología de la conservación utiliza el registro y análisis del pasado para desarrollar conocimiento, principios y herramientas para conservar y restaurar la biodiversidad y los servicios ecosistémicos frente al cambio climático actual y otros impactos antropogénicos (Birks, 2012; Dietl *et al.*, 2015; Dietl, 2016). El objetivo de la paleoecología es la reconstrucción de ambientes pasados, hábitats y ecosistemas, en el contexto de caracterizar la información general de un evento en particular, y reconstruir el clima del pasado con la intención de informar sobre los cambios climáticos y su efecto en el ambiente (Louys *et al.*, 2012), explorando la teoría ecológica en el tiempo geológico (Louys *et al.*, 2009; 2012).

Actualmente, se ha utilizado el registro fósil del Cuaternario porque provee una examinación directa de las hipótesis ecológicas, para las cuales estudios experimentales no son posibles por la limitación de la longevidad humana para la dinámica de los sistemas ecológicos bajo investigación (Delcourt y Delcourt, 1991). El Pleistoceno, la transición Pleistoceno-Holoceno y las fluctuaciones climáticas durante el Holoceno, son excelentes periodos de tiempo para estudiar la reacción de la biota frente a cambios climáticos importantes (Meadows, 2014). También, permite comparar el efecto de la biota con la ausencia y la presencia del hombre en Norte America (Seddon *et al.*, 2014; Jackson y Blois, 2015).

Los microvertebrados como los peces, anfibios, reptiles y mamíferos pequeños han mostrado características importantes, como su especialización a ciertos hábitats, condiciones ambientales y climáticas, permitiendo que sean útiles para la reconstrucción de ambientes y climas pasados (e.g. Bañuls-Cardona *et al.*, 2014; Blain *et al.*, 2014, 2015, 2016; Piñero *et al.*, 2015; Fernández-García *et al.*, 2016; López-García *et al.*, 2014, 2015, 2016; van Dam y Utescher, 2016). Los anfibios y reptiles pleistocénicos han sido poco estudiados en México y Centroamérica comparado con lo bien estudiados que están en Europa (Holman, 1998; Ratnikov, 2001; Szyndlar y Rage, 2002; Rage y Roček, 2003; Ivanov, 2007; Blain *et al.*, 2015) y Norteamérica (Holman, 1995, 2000, 2003, 2006). En México los estudios de fósiles de anfibios y reptiles son escasos comparados con los estudios paleomastozoológicos y están enfocados principalmente en taxonomía (Reynoso, 2006; Tovar-Liceaga y Montellano-Ballesteros, 2006). Por lo que el uso de la herpetofauna para reconstruir paleoclimas y paleoambientes no ha sido utilizada en México (Cruz, 2012).

Para reconstruir climas y ambientes pasados Eronen *et al.* (2010a) y Polly *et al.* (2011) mencionan que existen características funcionales de los organismos que reflejan las interacciones entre ellos y el medio abiótico que los rodea, llamadas ecométricos. Estas características pueden utilizarse como proxies para estudios paleoecológicos. Reconstrucciones paleoclimáticas utilizando a los vertebrados como proxy han sido realizadas utilizando diferentes métodos ecométricos como ecología térmica (Markwick 1994, 1998), relación entre tamaño-temperatura-tasa metabólica en poiquilotermos (Head *et al.*, 2009, 2013), relación entre grupos ecofisiológicos y el clima (Böhme 2003, 2004, 2008, 2010), funciones de transferencia (Hernández-Fernández y Peláez-Campomanes, 2005), la relación entre el clima y la diversidad (Montuire *et al.*, 1997, 2006; Legendre *et al.*, 2005; Escude *et al.*, 2013), los patrones de hipsodontia (Fortelius *et al.*, 2002, 2006; Eronen *et al.*, 2010b, 2011); intervalo climático mutuo (Blain *et al.*, 2007, 2009; Polly y Eronen, 2011; Smith y Polly, 2013) y la tafonomía (Holden *et al.*, 2013).

La estructura de las comunidades de anfibios y reptiles presentan una respuesta directa a las condiciones climáticas de temperatura y precipitación, así como una restricción ecológica a ciertos microambientes, además porque tienen una movilidad reducida (Araújo *et al.*, 2006, 2008; Gibbons *et al.*, 2000; Sinervo *et al.*, 2010; Vitt y Caldwell, 2014; Louys *et al.*, 2015). Además, los microvertebrados no alteran de manera sustancial los ambientes, como lo hizo la megafauna en el pasado al influir en la formación de comunidades vegetales no análogas con el presente (Guthrie, 1984; Johnson, 2009a, 2009b; Gill *et al.*, 2009, 2012, 2014; Faith, 2011). Esto permite que se pueda estudiar la estructura de las comunidades de vertebrados pequeños, a través del tiempo, como respuesta a los cambios ambientales y climáticos.

Cambios en las comunidades de mamíferos a través del tiempo han sido las más estudiadas, argumentando que los cambios en la estructura de las comunidades se deben principalmente a cambios climáticos (Blois y Hadly, 2009; Blois *et al.*, 2010; Royer *et al.*,

2016) o cambios de la estructura de la vegetación (Stegner y Holmes, 2013; Rowe y Terry, 2014; Stegner, 2016).

OBJETIVO

Comprender el dinamismo de las comunidades de anfibios y reptiles frente a cambios climáticos y ambientales a través del Cuaternario y con ello entender cómo se podrían comportar las comunidades a cambios climáticos y ambientales futuros.

HIPÓTESIS

Los cambios de la estructura de comunidades de anfibios y reptiles a través del tiempo son resultado principalmente de cambios en el clima (Blain *et al.*, 2015; Kemp y Hadly, 2016).

Los cambios de la estructura de comunidades de anfibios y reptiles a través del tiempo son resultado principalmente de cambios en la estructura de la vegetación (Bochaton *et al.*, 2015).

CAPÍTULO I

RECONSTRUYENDO EL PALEOAMBIENTE DE LA GRUTA DE LOLTÚN, YUCATÁN, MÉXICO, UTILIZANDO ANFIBIOS Y REPTILES PLEISTOCÉNICOS Y SUS IMPLICACIONES PALEOBIOGEOGRÁFICAS

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Reconstructing the paleoenvironment of Loltún Cave, Yucatán, Mexico, with Pleistocene amphibians and reptiles and their paleobiogeographic implications

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ABSTRACT

Loltún cave in Yucatán peninsula is an important fossil site. The cave preserves Pleistocene fauna and lithic tools, and it is among the few sites with amphibian and reptile fossils of the Mexican Pleistocene. We used the fossil amphibians and reptiles community to reconstruct the paleoclimate and paleoenvironment of Loltún cave in the Late Pleistocene. The Pleistocene amphibian and reptiles community in Loltún cave consists of one frog, three lizards, five snakes and one turtle. Applying the Habitat Weighting method to the fossil herpetofaunal assemblage, we inferred a vegetation mosaic non-analog with the present one, comprising evergreen seasonal forest, tropical deciduous forest and scrub forest, in contrast to the tropical semi-deciduous forest found nowadays around Loltún cave. Using the Mutual Climatic Range (MCR) method we inferred a mean annual temperature of 25.33 °C and a mean annual precipitation of 1183.74 mm; the temperature was 1.47 °C lower and the MAP was 85.14 mm higher than the present climate condition.

Is the first time that a paleoclimatic reconstruction using amphibians and reptiles in a tropical region is made using the MCR method. Our results are in concordance with other paleoclimatic inferences using fossil pollen as a proxy, extending the use of the MCR method to different climatic regions. We found a range shift of the iguanid *Ctenosaura* subgenus *Loganiosaura* during the Late Pleistocene, of 446.4 km north of the present distribution, surely given by the climatic and vegetation structure changes in the past.

Key words: Paleoclimate; paleoenvironment; amphibians; reptiles; Pleistocene; Yucatán peninsula.

RESUMEN

En la península de Yucatán, la gruta de Loltún es un sitio importante por la presencia de fauna pleistocénica junto con herramientas líticas. Este es uno de los pocos sitios con fósiles de anfibios y reptiles del Pleistoceno en el sur de México. Se utilizó la comunidad fósil de anfibios y reptiles para reconstruir el paleoambiente y paleoclima de la gruta de Loltún para el Pleistoceno Tardío, debido a que la herpetofauna presenta características importantes para la reconstrucción de ambientes pasados. La comunidad de anfibios y reptiles del Pleistoceno Tardío de la gruta de Loltún consiste en un anuro, tres saurios, cinco serpientes y una tortuga. Por medio de la aplicación del método de Ponderación de Hábitat para la comunidad herpetofaunística fósil, se pudo inferir que existió un mosaico de vegetación, no análogo con el presente, constituido de selva perennifolia, bosque tropical caducifolio y matorral xerófito, en contraposición al bosque tropical subcaducifolio presente en la actualidad. También, se infirió una temperatura promedio anual de 25.33 °C y una precipitación promedio anual de 1,183.74 mm, siendo 1.47 °C inferior y 85.14 mm superior a las condiciones climáticas actuales; para estas estimaciones se usó el método de Intervalo Climático Mutuo (ICM). Es la primera vez que se realiza una reconstrucción paleoclimática utilizando el método de ICM con anfibios y reptiles en una región tropical. Nuestros resultados concuerdan con las inferencias paleoclimáticas realizadas con polen fósil, extendiendo el uso del método ICM a diferentes regiones climáticas. Se infiere un cambio en la distribución de Ctenosaura subgénero Loganiosaura durante el Pleistoceno, 446.4 km más al norte de su distribución actual, lo cual seguramente fue producido por los cambios en la estructura de la vegetación y los cambios climáticos.

Palabras clave: Paleoclima; paleoambiente; anfibios; reptiles; Pleistoceno; península de Yucatán.

INTRODUCTION

The first study of amphibians and reptiles from the Pleistocene in Mexico was performed by Langebartel (1953) in many sites of the Yucatán peninsula. Langebartel (1953) reported six taxa of anurans, lizards and snakes and described two extinct species, an iguanid (*Ctenosaura premaxillaris*) and a xantusiid (*Lepidophyma arizeloglyphus*). Both species are still valid (Reynoso, 2006; Chávez-Galván *et al.*, 2013). Other herpetofaunal studies of the Pleistocene in southern Mexico include the description of *Trachemys* in Tabasco, *Trachemys*

Cruz, J.A., Arroyo-Cabrales, J., Reynoso, V.H., 2016, Reconstructing the paleoenvironment of Loltún Cave, Yucatán, Mexico, with Pleistocene amphibians and reptiles and their paleobiogeographic implications: Revista Mexicana de Ciencias Geológicas, v. 33, núm. 3, p. 342-354.

scripta, Kinosternon scorpioides and *Staurotypus* sp. in Chiapas (Luna-Espinoza and Carbot-Chanona, 2009), *Kinosternon hirtipes/integrum* and *Gopherus* sp. in Oaxaca (Cruz *et al.*, 2009) and *Claudius angustatus* and *Crocodylus* sp. in Veracruz (Peña-Serrano *et al.*, 2004).

One of the most intensively studied sites in the Yucatán peninsula is Loltún cave. The only sites in Mexico that have been systematically excavated with controlled stratigraphy are Loltún cave and San Josecito cave, Nuevo León (Arroyo-Cabrales and Polaco, 2003). Since the last years of the 1980 decade, the archaeological and paleontological significance of Loltún cave was emphasized by the discovery of Pleistocene fauna and lithic tools (Arroyo-Cabrales and Álvarez, 2003). It is one of the few sites in southern Mexico that has Pleistocene fossil amphibians and reptiles. The paleontological studies of Loltún cave have focused on mammals (Hatt, 1953; Álvarez and Polaco, 1972; Mercer, 1975; Cope, 1896; Álvarez and Arroyo-Cabrales, 1990; Arroyo-Cabrales and Álvarez, 1990, 2003), pollen (Xelhuantzi-López, 1986; Montúfar, 1987), mollusks (Álvarez and Polaco, 1972), birds (Fisher, 1953) and amphibians and reptiles (Langebartel, 1953).

Amphibians and reptiles can be good paleoecological proxies because they are ecologically, ethologically and physiologically restricted to microhabitats and specific environments, and many species have restricted geographic intervals and are territorial (Vitt and Caldwell, 2014). These animals are specialized to certain climatic conditions allowing the reconstruction of environments from past climates (Holman, 1995; Blain *et al.*, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016). In this study, fossil amphibian and reptile remains from Loltún cave were analyzed in order to infer 1) the site paleoenvironment and paleoclimate and 2) the changes in the amphibian and reptile communities during the Late Pleistocene in the Yucatán peninsula.

Loltún cave

Loltún cave is located in the southwest portion of the state of Yucatán (México), about 110 km south of Mérida and 7 km southwest from Oxcutzcab, at an elevation of 40 m a.s.l. Its geographic coordinates are 20°15'14.35" N and 89°27'20.82" W (Figure 1). The site is located on the foothills of the sierra de Ticul, in a karst region with several types of solution features exposed in Miocene rocks (Arroyo-Cabrales and Álvarez, 2003). Loltún cave is an east-west-oriented series of tunnels and chambers. It has nine chambers of which Loltún and Nahkab are used as the beginning of a tourist route. The excavations from which the fossil material for this study was obtained were made in the Huechil chamber (*Huech* means armadillo in maya language) (Arroyo-Cabrales and Álvarez, 1990).

The excavations were carried out using a metric grid and controlled stratigraphy during four seasons between 1977 and 1981. The levels or layers of the sequence can be divided into three main groups (Figure 2) (Schmidt, 1988; Arroyo-Cabrales and Álvarez, 2003):

Group 1. Levels I to VII are from the Ceramic Stage, but extinct animal remains are found in the bottom of level VII.

Group 2. Level VIII is from the Pre-Ceramic Stage; it includes some lithic elements and extinct fauna.

Group 3. Levels IX to XVI are Pleistocene in age, without any

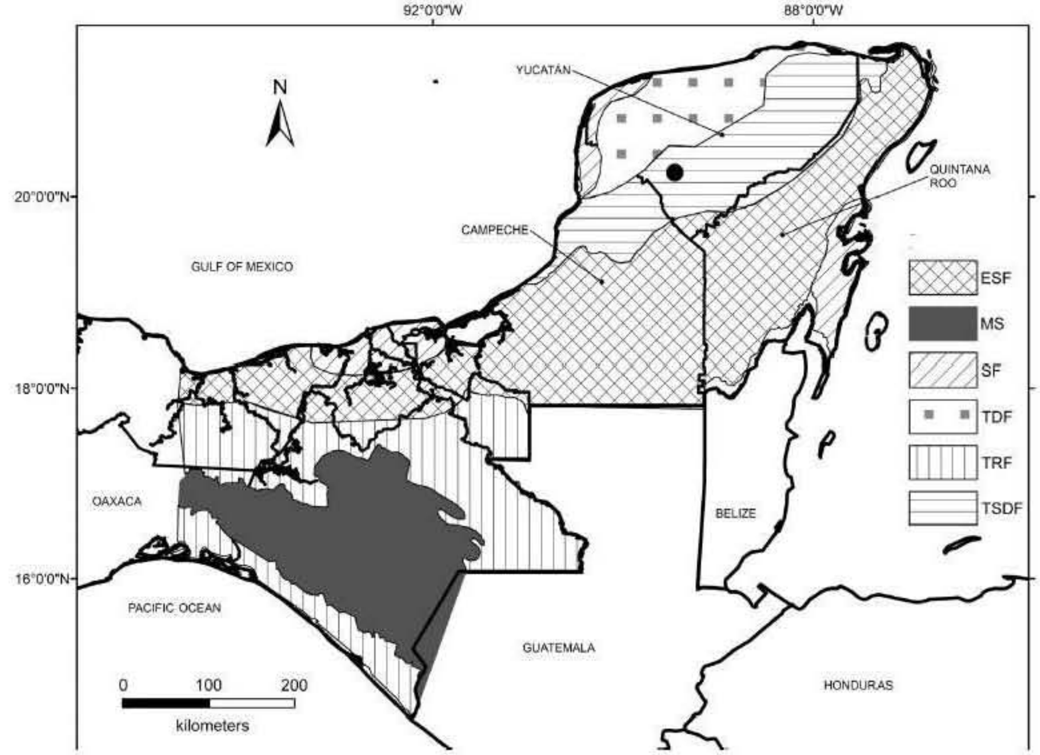

Figure 1. Loltún cave in Yucatán (black point). Habitat types found in the Yucatán peninsula and north Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS). Modified map from Correa-Metrio *et al.* (2011).

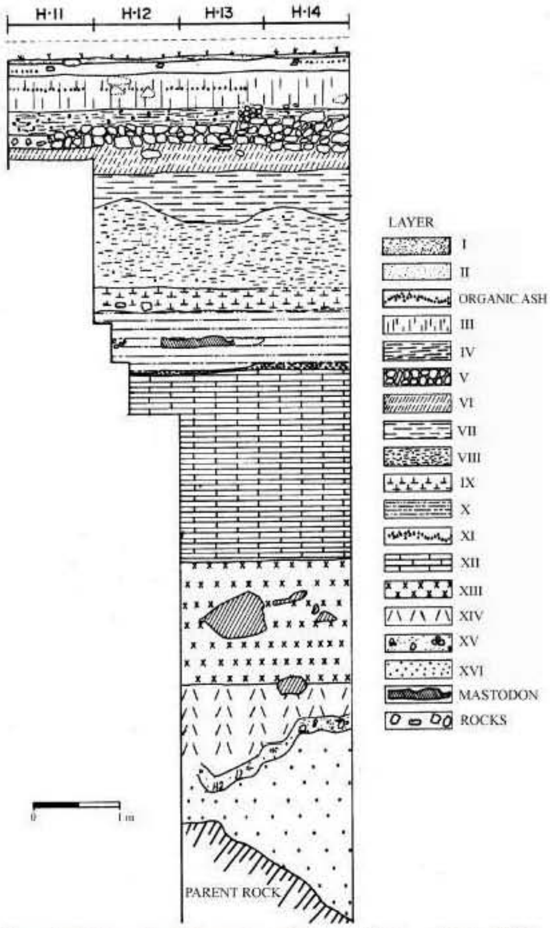

Figure 2. Stratigraphy (redrawn from Álvarez and Polaco, 1972) of El Toro Unit, Loltún cave, Yucatán peninsula. H 11-14, excavation boxes. Layer I, dark brown sediment; Layer II, light brown sediment; Layer III, dark brown sediment; Layer IV, dark brown sediment with rocks; Layer V, bed rocks; Layer VI, dark red sediment; Layer VII, red sediment; Layer VIII, light red sediment; Layer IX, dark red sediment; Layer X, light red sediment; Layer XI, volcanic ash (Rosseau tephra); Layer XII, red sediment; Layer XIII, compacted dark red sediment; Layer XIV, dark red sediment; Layer XV, compacted dark red sediment; Layer XVI, yellow red clay.

cultural material. Volcanic ash correlated to the Rosseau tephra was dated as 28,400 yrs BP by radiocarbon method (uncalibrated, Rampino *et al.*, 1979) and 32782 ± 296 cal yrs BP (Danzeglocke, 2007), and occurs in level XI.

MATERIALS AND METHODS

Fossil remains

The amphibian and reptile fossils studied were found in Loltún cave in the sequences reported as Group 3 which comprises levels XII to XVI, which are older than 32782 ± 296 cal yrs BP (Rampino *et al.*, 1979; Arroyo-Cabrales and Álvarez, 2003). The fossil remains were compared to reference osteological material from the Laboratorio de Arqueozoología "M. en C. Ticúl Álvarez Solórzano", Instituto Nacional de Antropología e Historia (DP) and the Colección Nacional de Anfibios y Reptiles, Universidad Nacional Autónoma de México (CNAR). The bones were identified using the criteria given by Holman (2003) for anurans, Auffenberg (1963), LaDuke (1991) and Holman (2000) for snake vertebrae and their regionalization, Evans (2008) for lizards and Preston (1979) for turtles. The remains were labeled as LC (Loltún cave), number of excavation and the level in roman numbers from which the material was obtained.

Paleoenvironmental reconstruction

In order to reconstruct the paleoenvironment, we used the Habitat Weighting Method with six different types of habitats found in the Yucatán peninsula and northern Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS), described by Correa-Metrio *et al.* (2011) (Figure 1). This method consists in establishing, first, the present-day habitat distribution of each amphibian and reptile taxon. Each species receives a score for each habitat type proportional to habitat preference; the sum of scores for all habitat types for each species is 1 (Blain *et al.*, 2008). The reconstruction of the paleoenvironment at the study site during the Late Pleistocene was determined by summing the scores of each habitat type for all species. The habitat type with the highest score is interpreted as the predominant habitat type.

Paleoclimatic reconstruction

The Mutual Climatic Range (MCR) method was used to reconstruct the Late Pleistocene paleoclimate around Loltún cave. This method consists in calculating the potential paleoclimatic conditions by identifying the geographic region where all the species in the locality or in a stratigraphical level currently live (Blain *et al.*, 2009). It is assumed that the overlapping areas of the current distribution of each taxon occurring in the locality contain the climatic conditions that were present in the past; in other words, the climatic conditions that were present in the locality where the fossil community was found, are represented by the overlapping of the current distributions.

For each fossil taxon a species distribution model (SDM) was constructed. To accomplish this, locality data from natural history collections such as Sistema Nacional de Información sobre la Biodiversisdad (CONABIO, www.conabio.org.mx), the Global Biodiversity Information Facility (GBIF, www.gbif.org), data reported in literature (Lee, 1996, 2000; Campbell, 1999; Köhler, 2003, 2010) and the Colección Nacional de Anfibios y Reptiles (CNAR), Instituto de Biología, Universidad Nacional Autónoma de México, were used.

The SDMs were constructed using the MaxEnt v3.3 software (Phillips *et al.*, 2006), which allows the use of SDMs for exploring and predicting the taxon's distribution even when using a small sample size (Wisz *et al.*, 2008). For each species, ten distinct models were generated using the *bootstrap* sampling and each model was validated with 30% of the original records. To evaluate the model, the area under the curve (AUC) generated with the ROC technique (Receiver Operating Characteristic) was used. The potential distribution was obtained by reclassifying with the *10 percentile training presence* from the average of the ten models made for each species. As a result, a binary map was created showing the optimal climatic conditions (1 = optimal, 0 = not optimal) for each of the living taxa that represent the fossil amphibian and reptiles found in Loltún cave, Yucatán.

The values of mean annual temperature (MAT) and mean annual precipitation (MAP) for the Late Pleistocene in Loltún cave obtained with the mutual climatic range method were compared with Oxkutzab, Yucatán, the closest weather station to the Loltún cave (smn.cna.gob.mx).

RESULTS

From the fossil remains found in the Loltún cave, we were able to identify one amphibian (*Rhinella marina*), and two lizards (*Ctenosaura defensor* and *C. similis*). We also found fossils from one lizard that belongs to *Ctenosaura* subgenus *Loganiosaura;* five snakes from the genera *Boa, Coluber, Drymarchon, Lampropeltis* and *Leptophis*, and a turtle from genus *Trachemys*.

Systematic paleontology

Class Amphibia Blainville, 1816
Order Anura Fischer von Waldheim, 1813
Family Bufonidae Gray, 1825
Genus *Rhinella* Fitzinger, 1826

Rhinella marina **Linnaeus, 1758**
Figure 3

Rana marina Linnaeus, 1758, Systema Naturae, Ed. 10, 1:211.
Bufo marinus Schneider, 1799, Historia Amphibiorum Naturalis: 219.
Chaunus marinus Frost *et al.*, 2006, Bulletin of the American Museum of Natural History, 297:364.
Rhinella marina Pramuk *et al.*, 2008, Herpetologica, 63:211.

Description. The radio-ulna (LC 360-XII) is slightly constricted. It has a large quadrangular radio-ulnar foramen. Its Y element's process is in form of a spine. The separation between the radial process and the ulnar process is weak. The radial process is conserved up to the middle of the ulnar part. In dorsal view, the trochanter diverges at an angle of 90°. It has an ulnar keel. In lateral view, the anterior radio-ulna edge is slightly angled.

The seventh vertebra (LC 360-XII) has an oval cotyle with dorsal edges in a U-like form. The neural spine is thin and short. The separation between the prezygapophyseal articular facets is less than their width. The postzygapophyseal keel merges from the posterior neural spine. The neural arch is depressed and concave.

The astragalus (LC 359-XII) has a distal canal, a smooth torsion of the element, and a robust form. The distal epiphyses has a triangular cross-section.

Material. Left radio-ulna (LC 360-XII), a seventh vertebra (LC 360-XII) and a left astragalus (LC 359-XII).

Discussion. The size of the material can only be compared to big anurans of the country like *Rhinella marina* (DP 732), *Lithobates catesbeianus* (DP 5086) and *Lithobates megapoda* (CNAR 15686). The radio-ulna is referred to *Rhinella marina* because they share the following characteristics: a smooth constriction, a quadrangular radio-ulnar foramen, spine-like Y process, a short distance between the radial and ulnar process, a trochanter deviation of 90°, and a slightly angled anterior edge (Table 1). The seventh vertebra is referred to *R. marina* because of the presence of an oval cotyle with dorsal edges in U-like form and a thin and short neural spine. The separation between the

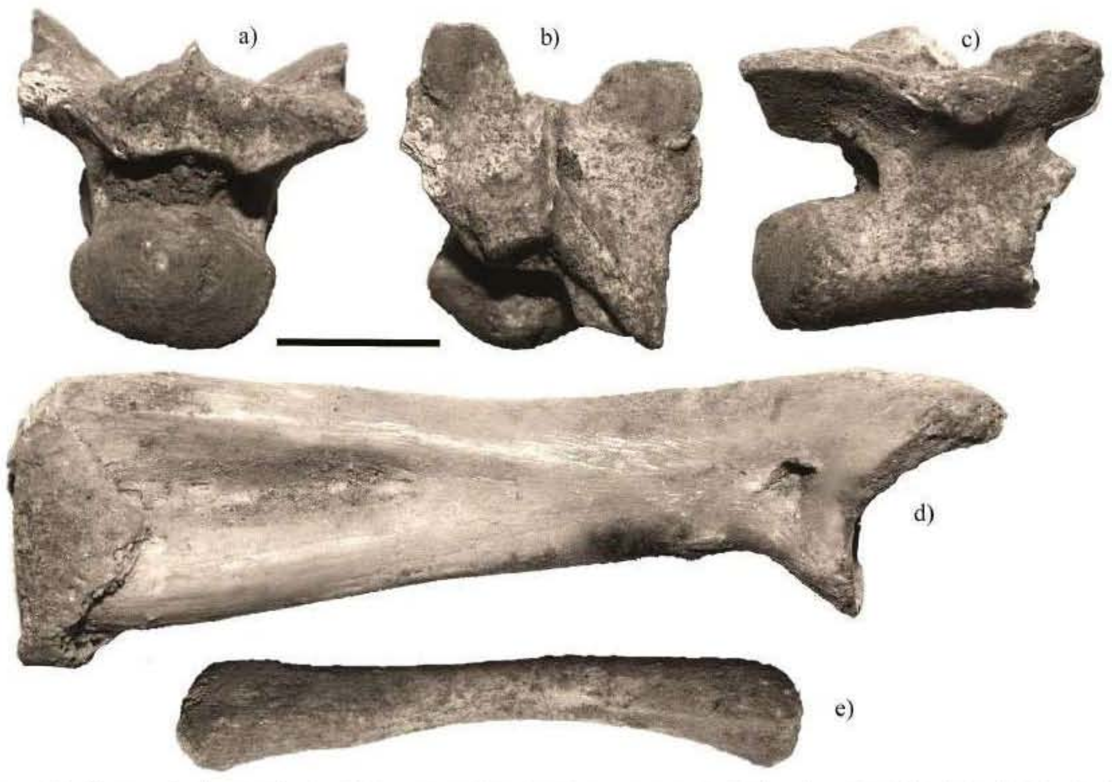

Figure 3. *Rhinella marina* fossil remains found in Loltún cave. Seventh trunk vertebra in posterior view (a), dorsal view (b) and lateral view (c). Left radio-ulna (d). Left astragalus (e). Scale bar = 5 mm.

Table 1. Comparison of radio-ulna between *Rhinella*, *Lithobates* and fossil material (LC 360-XII).

Feature	Genus		
	Fossil	*Rhinella*	*Lithobates*
Bone constriction	Unremarkable	Smooth	Strong
Ulnar and radial width	Equal	Slighlty narrow the anterior part	Narrow in the anterior part
Radio-ulnar foramen	Large and quadrangular	Small and quadrangular	Small and elongated
Y process	Like spine	Like spine	Underdeveloped
Distance between the radial and ulnar process	Close	Close	Broad
Trochanter deviation	90°	90°	Less than 90°
Anterior edge	Slightly angled	Slightly angled	Strongly angled

prezygapophyseal articular facets is short and a postzygapophyseal keel merges from the posterior neural spine (Table 2). The material described above is morphologically congruent with the osteological characters of *Rhinella marina*.

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Family Iguanidae Oppel, 1811
Genus *Ctenosaura* Wiegmann, 1828

Ctenosaura defensor Cope, 1866
Figure 4

Cachryx defensor Cope, 1866, Proceedings of the Academy of Natural Sciences of Philadelphia, 18:124.
Ctenosaura defensor Günther, 1890, Biologica Centrali-Americana, Reptilia and Batrachia: 58.
Enyaliosaurus defensor Smith and Taylor, 1950, Bulletin of the United States National Museum, 199:77.
Ctenosaura (*Enyaliosaurus*) *defensor* Köhler *et al.*, 2000, Amphibia-Reptilia, 21:188.

Description. The left dentary (LC 374-XIII) is small (19.8 mm). It has a closed Meckelian canal without sutures. This element shows 18 tooth positions, 14 of which preserve complete teeth. The teeth are pentacuspid.
Material. A left dentary (LC 374-XIII).
Discussion. The material here described can be confidently referred to *Ctenosaura defensor* on the basis of the characters discussed by de Queiroz (1987). A relevant character is the closed Meckelian canal without sutures present in all iguanids (Figure 4a). The identification is straightforward excluding the genus *Dipsosaurus* and some species of *Ctenosaura* (*C. acanthura*, *C. clarki*, *C. hemilopha*, *C. palearis*, *C. pectinata* and *C. similis*) because the teeth in these taxa have a maximum of four cusps. The presence of pentacuspid teeth is characteristic of *Ctenosaura defensor* and *Cyclura pinguis* excluding other polycuspid genus *Cyclura*, *Sauromalus* and *Iguana*) with six or more cusps. However, *C. pinguis* is excluded because it has a bigger dentary than *C. defensor*. The size of the latter is more consistent with the fossil remains.

Ctenosaura similis Gray, 1831
Figure 4

Iguana (*Ctenosaura*) *similis* Gray, 1831 *in* Griffith and Pidgeon (eds.), The animal kingdom arranged in conformity with its organization by the Baron Cuvier with additional descriptions of all species higher named, and of many before noticed, 38 p.
Ctenosaura similis Bailey, 1929, Proceedings of the United States National Museum, 73:32.
Ctenosaura (*Ctenosaura*) *similis* Köhler *et al.*, 2000, Amphibia-Reptilia, 21:187.

Material. A posterior fragment of the left maxilla (LC 367-XII-XIII), first and second sacral vertebrae (LC 367-XII-XIII, LC 360-XII), two cervical vertebrae (LC 361-XII), six trunk vertebrae (LC 357-XIII, 359-XII, 361-XII, 367-XII-XIII) and six caudal vertebrae (LC 357-XIII, 359-XII, 361-XII, 362- XII, 367-XII-XIII).
Discussion. The fossils were compared with recent osteological material of *Ctenosaura similis* and *C. pectinata*, without finding important differences in the maxilla or the trunk vertebrae. The fossil material is referred to *C. smilis* because they share the following characteristics: the sacral vertebra have a neural spine that overhangs dorsally, in the first sacral vertebra, the distal part of the pleurapophysis is large and flat and the condyle of the second sacral vertebra is dorsoventrally large. These characteristics differ from *C. pectinata*.

Genus *Ctenosaura* Wiegmann, 1828
Subgenus *Loganiosaura* Köhler *et al.*, 2000
Figure 4

Ctenosaura Stejneger, 1901, Proceedings of the United States National Museum, 23:467.
Enyaliosaurus Cochran, 1961, United States Natural Museum Bulletin, 1961:105.
Ctenosaura subgenus *Loganiosaura* Köhler *et al.*, 2000, Amphibia-Reptilia, 21:187.

Type species. *Ctenosaura bakeri* Stejneger, 1901.

Table 2. Comparison of the seventh vertebra between *Rhinella*, *Lithobates* and fossil material (LC 360-XII).

Feature	Genus		
	Fossil	*Rhinella*	*Lithobates*
Cotyle	Oval with dorsal edges U-like form	Oval with dorsal edges U-like form	Oval with convex dorsal edges
Neural spine	Thin and short	Thin and short	Thick and tall
Separation between prezygapophyseal articular facets	Short	Short	Wide
Postzygapophyseal keel	Merges from the posterior segment of neural spine	Merges from the posterior segment of neural spine	Merges from the anterior segment of neural spine

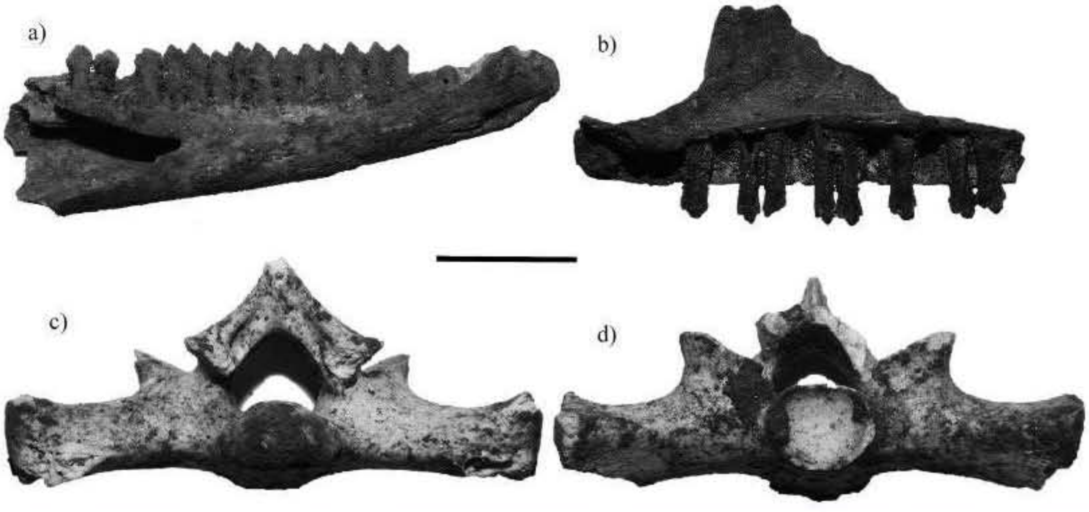

Figure 4. Fossil iguanid remains found in Loltún cave. *Ctenosaura defensor* left dentary (a). *Ctenosaura* subgenus *Loganiosaura* right maxilla (b). *Ctenosaura similis* sacral vertebra in posterior (c) and anterior view (d). Scale bar = 5 mm.

Description. A right maxilla. This element shows 16 tooth positions, eight of which preserved complete teeth. The teeth are tetracuspid. The anterior part of the maxilla has a ventral straight edge.

Material. Right maxilla (LC 359-XII).

Discussion. The genus *Ctenosaura* includes three subgenera: *Enyaliosarus, Ctenosaura* and *Loganiosaura* (de Queiroz, 1987). The subgenus *Enyaliosarus* is composed of *Ctenosaura quinquecarinata* complex (Hasbún *et al.*, 2005) which can be excluded because the species of this group have tricuspid teeth (*e.g. C. oaxacana*) or pentacuspid (*e.g. C. defensor*). Tetracuspid teeth are found in the subgenera *Ctenosaura* and *Loganiosaura*, of which the subgenus *Ctenosaura* is excluded because the anterior part of the fossil maxilla is straight (Oelrich, 1956; de Queiroz, 1987). The subgenus *Loganiosaura* is composed of four species, of which de Queiroz (1987) mentions that *C. bakeri* has tricuspid teeth and *C. palearis* tetracuspid teeth. There is no reference osteological material for the other two species, *C. melanosterna* and *C. oedirhina*, so the fossil remains were only identified at the subgenus level.

Family Boidae Gray, 1825

Genus *Boa* Linnaeus, 1758
Figure 5

Boa Linnaeus, 1758, Systema Naturae, Ed. 10, 1:215.

Constrictor Martin, 1958, Miscellaneous publications, Museum of Zoology, University of Michigan. 101:67.

Type species. *Boa constrictor* Linnaeus, 1758.

Material. Three cervical vertebrae (LC 363-XII, 372-XIII, 378-XVI), six anterior trunk vertebrae (LC 357-XIII, 370-XIII, 371-XIII) and four posterior trunk vertebrae (LC 360 XII, 362-XII, 370-XIII).

Discussion. The material can be referred to *Boa* on the basis of the character discussed, among others, by Holman (1981, 2000), Albino and Carlini (2008) and Albino (2011). The fossil vertebrae present diagnostic characters such as: robust, tall and short form; a tall neural arch and spine; small prezygapophyseal processes; diapophysis and parapophysis are slightly distinguished; cotyles and condyles are bigger than the neural canal; a robust zygosphene and the neural arch is clearly convex. Hynková *et al.* (2009) and Card *et al.* (2016) separated *Boa constrictor* into three species *B. constrictor, B. imperator* and *B. sigma*. There are no osteological studies available to separate the fossil material to a specific level, so the fossil remains were only identified at the genus level.

Family Colubridae Oppel, 1811

Genus *Drymarchon* Fitzinger, 1843
Figure 5

Drymarchon Boie, 1827, Bermerkungen über Merrem´s Versuch eines Systems der Amphibien, 1. Lieferung, Ophidier: Isis van Oken, 20, 508-566.

Coluber Boie, 1827, Bermerkungen über Merrem´s Versuch eines Systems der Amphibien, 1. Lieferung, Ophidier: Isis van Oken, 20, 508-566.

Spilotes melanurus Duméril, Bibron and Duméril, 1854, Erpétologie Genérale ou Histoire Naturelle Complète des Reptiles, 9, 224.

Drymarchon Stuart, 1935, University of Michigan Museum of Zoology Miscellaneous Publications 29: 49.

Type species. *Drymarchon corais* Boie, 1827.

Material. Seven anterior trunk vertebrae (LC 356-XII, 359-XII, 361-XII, 364-XII, 374-XIII) and two posterior trunk vertebrae (LC 360-XII, 361-XII).

Discussion. The material can be referred to *Drymarchon* on the basis of the characters discussed by Auffenberg (1963) and Holman (2000). The fossil vertebrae present relevant characters such as, evident subcentral bridges, in ventral view the centrum is subtriangular; a gladiate hemal keel; epizygapophyseal spines and in posterior and dorsal view the accessory processes overhang laterally. Molecular studies (Wüster *et al.*, 2001) separated *D. corais* into three species *D. corais, D. melanurus* and *D. caudomaculatus* so that new osteological studies should be performed to identify our fossil remains to a specific level.

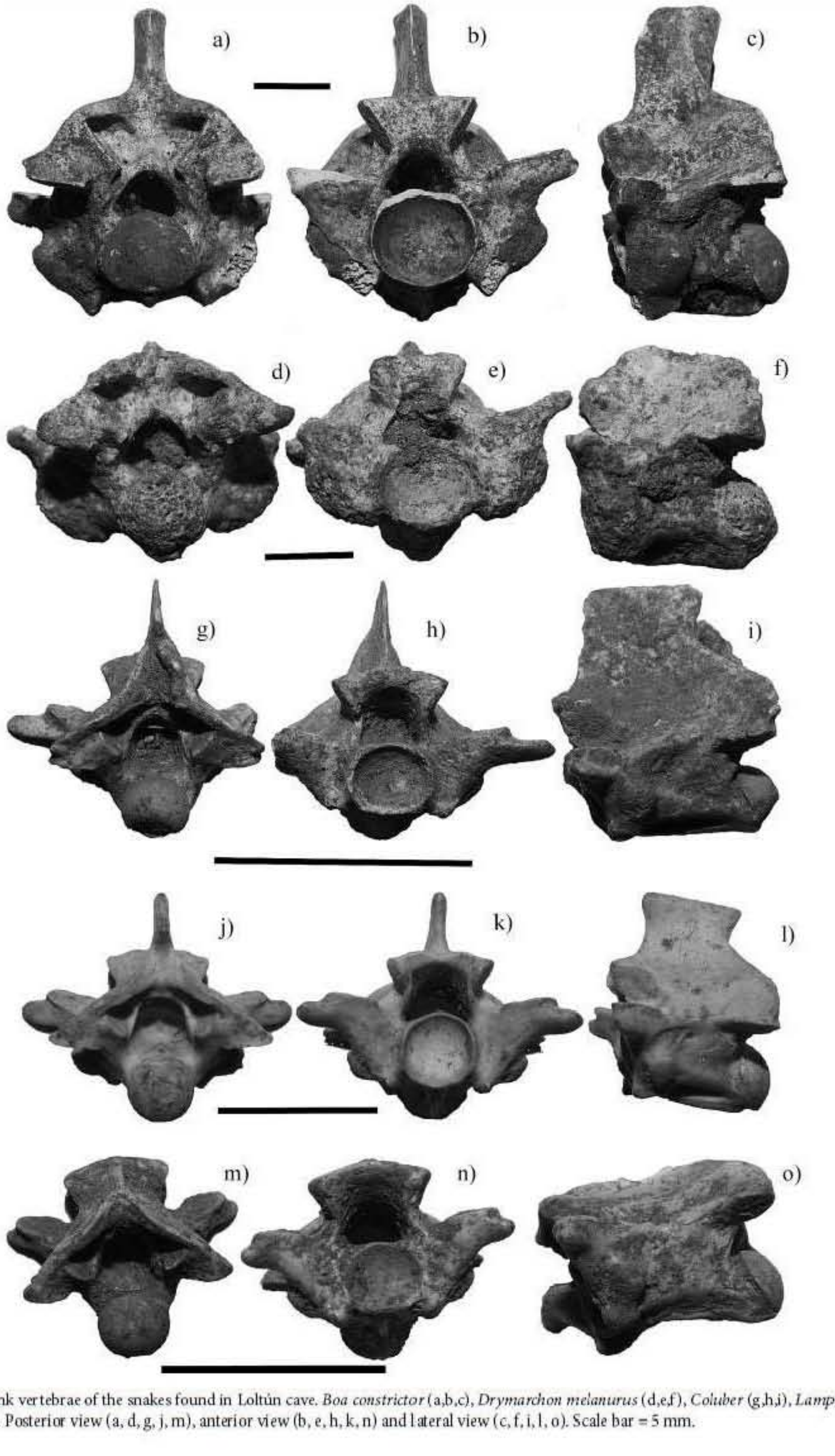

Figure 5. Fossil trunk vertebrae of the snakes found in Loltún cave. *Boa constrictor* (a,b,c), *Drymarchon melanurus* (d,e,f), *Coluber* (g,h,i), *Lampropeltis* (j, k, l), and *Leptophis* (m, n, o). Posterior view (a, d, g, j, m), anterior view (b, e, h, k, n) and lateral view (c, f, i, l, o). Scale bar = 5 mm.

Genus *Coluber* (*Masticophis*) Baird and Girard 1853

Figure 5

Leptophis Hallowell, 1852, Proceedings of the Academy of Natural Sciences of Philadelphia, 6:181.

Masticophis Baird and Girard, 1853, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution, 103.

Coluber Utiger *et al.*, 2005, Russian Journal of Herpetology, 12:51.

Type species. *Coluber constrictor* Linnaeus, 1758.

Material. An anterior trunk vertebra (LC 362-XII).

Discussion. Meylan (1982), LaDuke (1991) and Holman (2000) mention that the differences between the vertebrae from *Masticophis* and *Coluber* are not clear. Molecular studies have supported the synonymy of the genus *Masticophis* with *Coluber* (Utiger *et al.*, 2005), giving a possible explanation for the osteological similarity of the vertebrae between these genera. Despite this, Auffenberg (1963), Meylan (1982) and LaDuke (1991) identify the genus *Masticophis* on the basis of the following characteristics: long vertebrae with convex neural arch; a subquadrangular neural canal with a dorsal edge smaller than the ventral one; round postzygapophyseal articular facets; long, thick and blunt accessory processes; slightly developed subcentral ridges; gladiate hemal keel and epizygapophyseal spines. The fossil remain presents all of the characteristics mentioned above allowing us identify it as the genus *Masticophis*.

Genus *Lampropeltis* Linnaeus, 1766

Figure 5

Coluber Linnaeus, 1766, Systema Naturae per regna tria nature, secundum clases, ordines, genera, species, cum characteribus differentiis, synonymis, locis: 328.

Herpetodryas Schlegel, 1843, Essay on the physiognomy of serpents: 152.

Ophibolus Baird and Girard, 1853, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution, 85.

Coronella Duméril, Bibron and Duméril, 1854, Erpétologie Genérale ou Histoire Naturelle Complète des Reptiles, 9:616.

Triaeniopholis Werner, 1924, Gedruckt mit Unterstützung aus dem Jerome und Margaret Stonborough-Fonds, 133:50.

Lampropeltis Pyron and Burbrink, 2009, Zootaxa, 2241:24.

Type species. *Lampropeltis getula* Linnaeus, 1766.

Material. A cervical vertebra (LC 366-XII), four anterior trunk vertebrae (LC 359-XII, 366-XII, 372-XIII) and a posterior trunk vertebra (LC 356-XII).

Discussion. Genus *Lampropeltis* is diagnosed by the following characteristics: vertebrae are wider than long; a strongly depressed neural arch; cotyle is bigger than the neural canal; moderately blunt accessory processes; slightly developed subcentral ridges; thin and gladiate hemal keel and it does not have epizygapophyseal spines (Auffenberg, 1963, Meylan, 1982; Holman, 2000). The fossil remains present all of the characteristics mentioned above allowing us identify them as genus *Lampropeltis*.

Genus *Leptophis* sp. Linnaeus, 1758

Figure 5

Coluber Linnaeus, 1758, Systema Naturae, Ed. 10, 1:225.

Leptophis Bell, 1825, Zoological Journal, London, 2:328.

Ahaetulla Gray, 1831, *in* Griffith and Pidgeon, The animal kingdom arranged in conformity with its organisation by the Baron Cuvier with additional descriptions of all the species higher named, and of many before noticed, 93.

Dendrophis Schlegel, 1837, Essai sur la physionomie des serpens, 224.

Type species. *Leptophis ahaetulla* Linnaeus, 1758.

Description. Long, narrow and flattened vertebrae. In anterior view, the cotyles are laterally subrounded, slightly bigger than the neural canal; a convex zygosphene; short accessory processes that overhang laterally. In posterior view, the neural arch is convex and slightly flattened; it has a keel between the parazygantral facet and the postzygapophyseal articular facet; circular condyle. In dorsal view, the zygosphene is convex; rounded, subtriangular or oval prezygapophyseal articular facets; short, wide and rounded accessory processes; the neural spine is no longer than the posterior part of the neural arch. In ventral view, the anterior trunk vertebrae have a short gladiate hemal keel which is only evident in the posterior part of the centrum; the posterior trunk vertebra does not have a hemal keel. It has a long subtriangular to cylindrical centrum; the articular postzygapophyseal facets are rounded or subtriangular; weak or absent subcentral ridges. In lateral view, interzygapophyseal ridges are absent; the neural spine is long and short and the anterior edge beveled; and centrum deeply concave.

Material. Two anterior trunk vertebrae (LC 57-XIII, 359-XIII) and a posterior trunk vertebra (LC 359-XII).

Discussion. *Leptophis* Pleistocene fossil remains are here described for the first time for México (Chávez-Galván *et al.*, 2013). Osteological studies of *Leptophis* have focused on the skull (Oliver, 1948; Wilson, 1970; Souza and Lema, 1990) making this study the first one to describe *Leptophis* vertebrae. The vertebrae are characterized by a concave centrum and a hemal keel in the posterior part. We could only identify the fossil remains as *Leptophis* because only *L. mexicanus* had reference osteological material.

Order Testudines Batsch, 1788

Family Emydidae Rafinesque, 1815

Genus *Trachemys* Agassiz, 1857

Figure 6.

Trachemys Agassiz, 1857, Contributions to the Natural History of the United States of America, North American Testudinata, 252.

Callichelys Gray, 1863, Annals and Magazine of Natural History 13:181

Redamia Gray, 1870, Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Testudinata, 35.

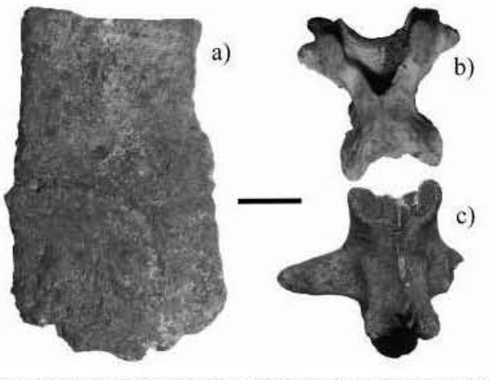

Figure 6. *Trachemys* fossil remain found in Loltún cave. Ninth peripheral bone (a), cervical vertebra (b) and caudal vertebra (c). Scale bar = 5 mm.

Type species. *Trachemys terrapen* Bonnaterre, 1789.

Description. Fragment of the ninth right peripheral bone. In exterior view, imprints of the ninth and tenth marginals scutes are present. The fifth costal can be seen in the upper part. In the visceral surface, the characteristic bulge of the last scutes with a small central foramen can be seen.

Material. Ninth right peripheral bone (LC 356-XII), two cervical vertebrae (LC 360-XII, 363-XII) and a caudal vertebra (LC 362-XII).

Discussion. The ninth right peripheral was compared with reference osteological material of *Rhinoclemmys* and *Trachemys* assigning the fossil material to *Trachemys* because it only has one mark (Souza *et al.*, 2000). It cannot be assigned to Kinosternidae because it does not present a vermiform ornamentation (Cadena *et al.*, 2007) nor elevated imprints of the ninth and tenth marginals (Preston, 1979). The vertebrae did not have morphological features that helped with the identification.

Pleistocene amphibians and reptiles

Amphibian and reptile remains from Loltún cave are here described finding six new taxa for this site: *Ctenosaura defensor*, *C.* (*Loganiosaura*) sp., *Boa* sp., *Lampropeltis*, *Leptophis* and *Trachemys* (Table 3). *Ctenosaura defensor*, *C.* (*Loganiosaura*) sp. and *Leptophis* are here reported for the first time for the Pleistocene in México and North America. Nowadays, *C.* (*Loganiosaura*) sp. is not found in the Yucatán peninsula. For the Pleistocene herpetofauna of southern México, Loltún cave is now the most studied site.

Paleoclimatic and paleoenvironmental reconstruction

The habitat types that have the highest score (1.9) obtained by the habitat weightings method are evergreen seasonal forest (ESF), tropical deciduous forest (TDF) and scrub forest (SF) (Table 4), suggesting that these habitat types were found at the study site during the Late Pleistocene. This mosaic differs from the vegetation structure of tropical semi-deciduous forest (TSDF) found today in the Loltún cave (Correa-Metrio *et al.*, 2011) and indicates that the paleoenvironment for Loltún cave had a vegetation mosaic not analogous with the present one.

The inferred paleoclimate for the Late Pleistocene in Loltún cave indicates climate conditions proper of the north and west part of the Yucatán peninsula with ESF, TDF and SF habitat types. This shows that for the Late Pleistocene, older than 32782 ± 296 cal yrs BP, Loltún cave had a MAT of 25.33 ± 0.47 °C and an MAP of 1,183.74 ± 143.35 mm.

Table 3. Taxa from the Pleistocene of the Loltun Cave. [a] Current names taken from Uetz *et al.* (2015).

Langebartel (1953)	**Current names**[a]	**This study**
Bufo ?horribilis	*Rhinella marina*	*Rhinella marina*
Ctenosaura ?similis	*Ctenosaura similis*	*Ctenosaura similis*
?Drymarchon corais	*Drymarchon melanurus*	*Drymarchon sp.*
Elaphe ?flavirufa or *E. ?triaspis*	*Pseudoelaphe flavirufa* or *Senticolis triaspis*	-
Masticophis ?mentovarius	*Coluber mentovarius*	*Coluber* subgenus *Masticophis*
Crotalus or *Bothrops*	*Crotalus* or *Bothrops*	-
		Ctenosaura defensor *Ctenosaura* subgenus *Loganiosaura* *Boa sp.* *Lampropeltis* sp. *Leptophis* sp. *Trachemys* sp.

Table 4. Habitat weighting analysis using amphibians and reptiles assemblage from Loltún cave, Yucatán. TRF, tropical rainforest; ESF, evergreen seasonal forest; TSDF, tropical semi-deciduous forest; TDF, tropical deciduous forest; SF, scrub forest; MS, montane systems.

	TRF	**ESF**	**TSDF**	**TDF**	**SF**	**MS**
Rhinella marina	0.167	0.167	0.167	0.167	0.167	0.167
Ctenosaura defensor		0.5		0.5		
Ctenosaura similis	0.2	0.2	0.2	0.2	0.2	
Ctenosaura (*Loganisaura*)					0.5	0.5
Boa	0.167	0.167	0.167	0.167	0.167	0.167
Coluber (*Masticophis*)	0.167	0.167	0.167	0.167	0.167	0.167
Drymarchon	0.167	0.167	0.167	0.167	0.167	0.167
Lampropeltis	0.167	0.167	0.167	0.167	0.167	0.167
Leptophis	0.167	0.167	0.167	0.167	0.167	0.167
Trachemys	0.2	0.2	0.2	0.2	0.2	
Total	1.4	1.9	1.4	1.9	1.9	1.5

These values when compared with the values given by Oxcutzcab weather station suggest that the MAT during the Late Pleistocene was -1.47 °C lower and the MAP was 85.14 mm higher than today conditions (Table 5).

DISCUSSION

Loltún cave is an important site in southern México, where 12 taxa of Pleistocene amphibians and reptiles have been found and described (Langebartel 1953; this study). A fewer taxa have been described in other places, for example, in Tabasco, one turtle (Luna-Espinoza and Carbot-Chanona, 2009); in Chiapas, three turtles (Luna-Espinoza and Carbot-Chanona, 2009); in Oaxaca, two turtles (Cruz *et al.*, 2009), and in Veracruz, one turtle and a crocodile (Peña-Serrano *et al.*, 2004).

The results suggest a paleoenvironment composed of a vegetation mosaic, different of the present one, with three habitat types: evergreen seasonal forest (ESF), tropical deciduous forest (TDF), and scrub forest (SF). Vegetation communities non-analog with the present ones have been reported in Petén Itza lake, in the Yucatán peninsula (Correa-Metrio *et al.*, 2012a, 2012b), which agree with our findings.

The paleoclimate reconstruction infers a MAT 1.47 °C lower and an MAP 85.14 mm higher than the present one. Since 65 ka BP to LGM (22 ka), Correa-Metrio *et al.* (2012a) suggest that the MAT decreased 1.5 °C compared with today. Periods of lower humidity occurred during the Heinrich Stadials (Correa-Metrio *et al.*, 2012a) suggesting that the period of the fossil remains in Loltún cave is an interglacial before the LGM (Correa-Metrio *et al.*, 2012a).

The distribution of *Ctenosaura* subgenus *Loganiosaura* suffered changes during the Pleistocene. Today, *Loganiosaura* is found in tropical rainforest areas (TRF) and montane systems (MS) (Köhler, 2003). This study shows that in the past this species could be found in Loltún cave, 446.4 km further to the north than its present distribution (Figure 7). This range shift has been found also for the skunk (*Mephitis macroura*) and the wolf (*Canis lupus*) (Arroyo-Cabrales and Álvarez, 2003) that, like *Loganiosaura*, are not found today in the Yucatán peninsula (Sosa-Escalante *et al.*, 2014). During the Late Pleistocene, *Mephitis macroura* and *Canis lupus* were found 489.78 km and 714.94 km further northeast (García-Moreno *et al.*, 1996; Hwang y Larivière, 2001) (Figure 7). The changes in the distribution of these species could be caused by the isotherm displacement which is calculated for the region between 179 to 250 m/yr for the 38-29 ka time interval (Correa-Metrio *et al.*, 2013).

Table 5. Paleoclimatic reconstruction in Loltún cave, Yucatán, using Mutual Climatic Range method, and compared with Oxkutzcab, Yucatán, the closest weather station to Loltún cave. MAT, mean annual temperature; MAP, mean annual precipitation; sd, standard deviation.

	Oxkutzcab	**Loltún**	**sd**	**Minimum**	**Maximum**	**Difference**
MAT	26.8	25.33	±0.47	25	26	-1.47
MAP	1,098.6	1,183.74	±143.35	968	1,490	+85.14

CONCLUSIONS

The Loltún cave is now the most studied site of southern Mexico because of amphibian and reptile fossils found there. In Loltún cave, the herpetofaunal community is a good paleoenvironment and paleoclimate indicator for the Late Pleistocene and shows a decrease in the MAT, and an increase in the MAP, suggesting an interglacial period before the LGM. In the past, the habitat type was a mosaic vegetation composed of evergreen seasonal forest (ESF), tropical deciduous forest (TDF), and scrub forest (SF). The paleoenvironment for Loltún cave shows a mixture of habitat types, not found today in the area. Climate and vegetation composition changes during the Late Pleistocene could have affected the distribution of *Ctenosaura* subgenus *Loganiosaura* and of other species, such as mammals.

Implementing the MCR method, using amphibians and reptiles as paleoclimatic proxies, allowed us to compare and evaluate this method, and to find trends of past climates and how they affect different organisms. It is the first time that a paleoclimatic reconstruction using amphibians and reptiles in a tropical region is made using the MCR method. Our results are in concordance with other paleoclimatic inferences using fossil pollen as a proxy, extending the use of the MCR method to different climatic regions.

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SUPPLEMENTARY MATERIAL

Supplementary Figure S1 "Overlapping area (black area) inhab-

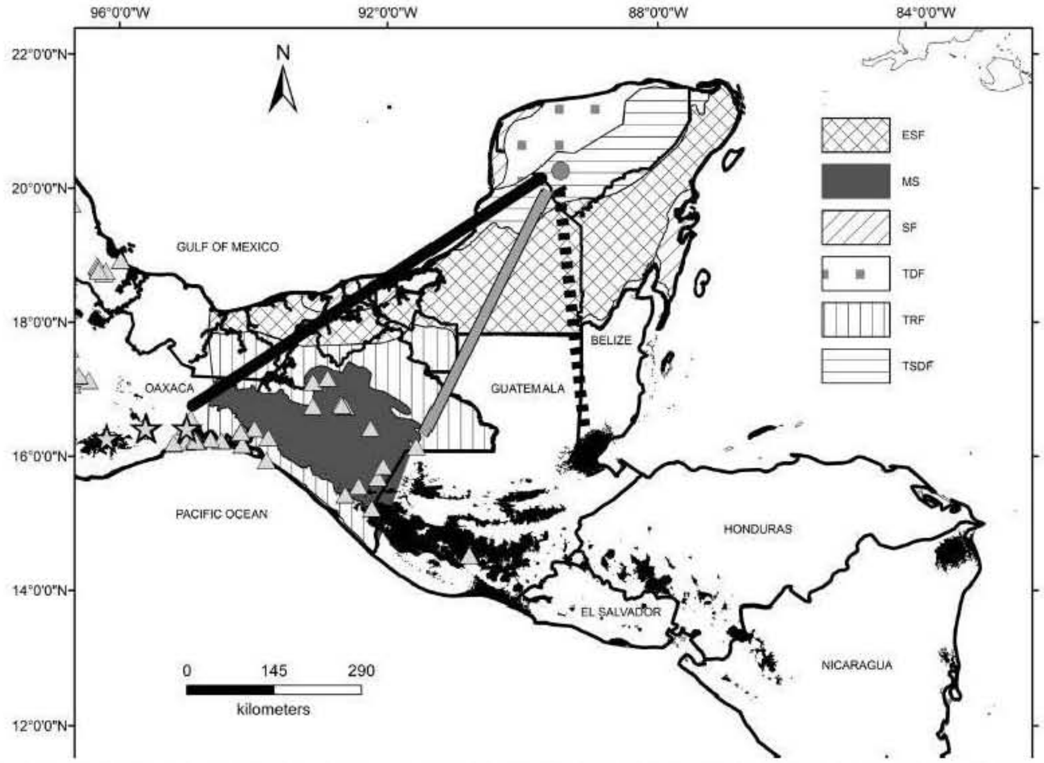

Figure 7. Present distribution of *Ctenosaura* subgenus *Loganiosaura* (black area), *Mephitis macroura* (grey triangles), historic distribution of *Canis lupus baileyi* (grey stars) and their changes in distribution during the Late Pleistocene in Loltún cave (gray point). Distance of changes are shown as dotted line for *Ctenosaura* subgenus *Loganiosaura*, gray line for *Mephitis macroura* and bold line for *Canis lupus baileyi*. Habitat types found in the Yucatán peninsula and Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS). Modified map from Correa-Metrio *et al.* (2011).

ited by the species of amphibians and reptiles from Loltún cave" and Supplementary File 1 "Georeferenced data of the actual representatives of fossil taxa founded in Loltún cave" can be found at the journal web site <http://rmcg.unam.mx/>, in the table of contents of this issue.

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SUPPLEMENTARY FILE 1

to the paper

Reconstructing the paleoenvironment of Loltún Cave, Yucatán, México, with Pleistocene amphibians and reptiles and their paleobiogeographic implications

by

José Alberto Cruz, Joaquín Arroyo-Cabrales, Víctor Hugo Reynoso

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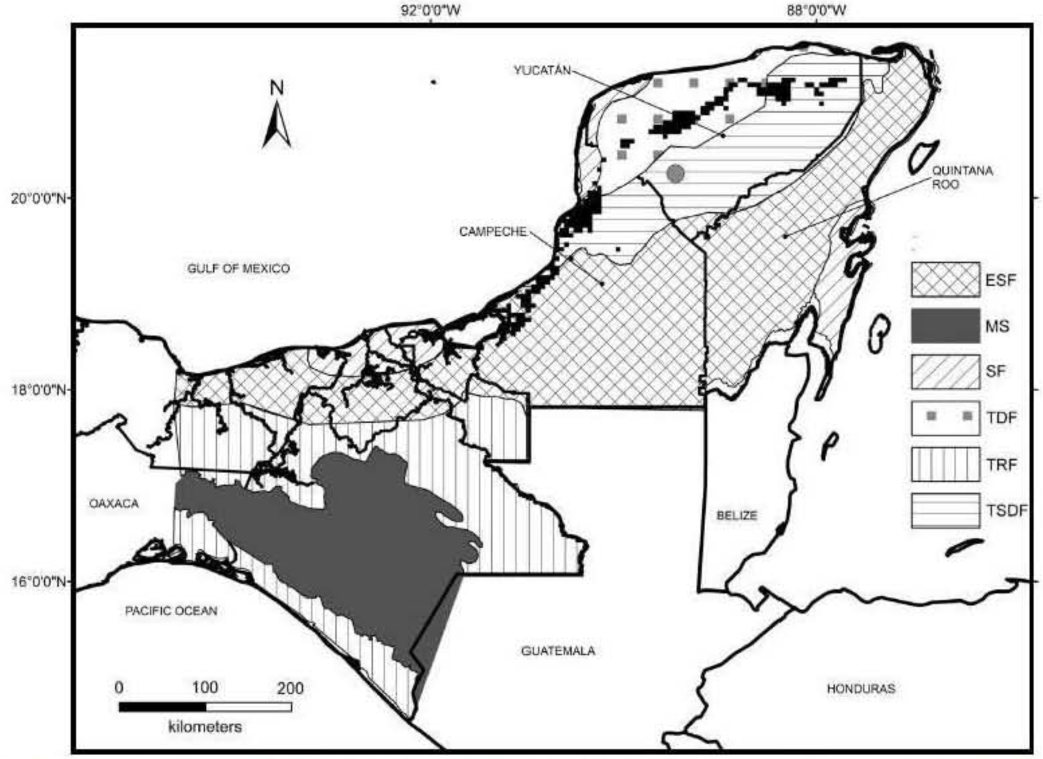

Figure S1. Overlapping area (black area) inhabited by the species of amphibians and reptiles from Loltún cave. Values of the area are 1 and 11 from Table S1 (see the second file of this supplement).

CAPÍTULO II

IMPLICACIONES EN LA PALEODRITRIBUCIÓN Y PALEOECOLOGÍA DE REPTILES ESCAMOSOS PLEISTOCÉNICOS DE NUEVO LEÓN, MÉXICO

(*Quaternary International:* Enviado*)*

Paleodistributional and paleoecological implications of Pleistocene Squamata in Nuevo León, México

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Abstract

San Josecito Cave (SJC) is one of the best studied Pleistocene paleontological localities in Mexico, with a strict stratigraphical control and several radiocarbon dating. Squamate fossil remains from layer 720 have an estimated age of 32673 ± 889 calendar years BP (28005 ± 1035 C^{14} years BP). *Barisia ciliaris, Phrynosoma modestum, Heterodon simus*, *Tantilla,* and *Storeria* are the first reports for the Pleistocene in Mexico. The presence of *Heterodon simus* in San Josecito indicates a post-Pleistocene reduction of its distribution range to eastern North America (USA and Canada) being the southernmost range of the species. The presence of *P. modestum* and *B. imbricata* indicates a post-Pleistocene reduction of their distribution range. For *P. modestum*, the reduction is related to elevation, occurring today in the State of Nuevo Leon at lower elevations in the Mexican Plateau. For *B. imbricate*, the range shift is to the Transmexican Volcanic Belt, the occurrence being the northernmost record of *B. imbricata*. A Weighting Habitat analysis indicated that open oak-pine forests and savanna surrounded SJC. Simpatry of *B. ciliaris* and *B. imbricate* in SJC indicates a colder and humid climate at the end of the Pleistocene in the cave area. These climatic conditions are found in the current sympatric area distribution of the species 450 km to the south of SJC.

Keywords: Paleoenvironment; palaeobiogeography; Pleistocene; Squamata; Mexico

1. Introduction

Small vertebrates, like micromammals, birds, amphibians, reptiles, and fish, have shown important characteristics for past environmental reconstruction (Holman, 1995; Legendre *et al.*, 2005; Blain *et al.*, 2008, 2009). Amphibian and reptiles respond in a strict manner to the environment and its changes. They are ecologically, ethologically, and physiologically restricted to specific microhabitats and environments and several forms have quite small geographic intervals and could be territorial (Vitt and Caldwell, 2014). These characteristics are important as fossil markers. Their specialization to some environments, allowing the reconstruction of past climates (Blain *et al.*, 2008, 2009, 2010, 2011, 2012, 2013).

Distributional changes usually are explained by the niche conservationist theory that proposes that the niche is kept with the ecological requirements of the organisms throughout the time (Wiens *et al.*, 2010). Pleistocene distribution changes may be due to taxa movements in order to conserve their niches rather than adapting to new conditions (Martínez-Meyer *et al.*, 2004; Hadly *et al.*, 2009). This pattern has been observed with recent amphibians and reptiles (e.g. Pyron and Burbrink, 2009; Rödder and Lötters, 2009; Kozak and Wiens, 2010; Pearman *et al.*, 2010), and here the niche conservationist theory is considered to understand the palaeoecology and palaeodistribution of Mexican Pleistocene amphibians and reptiles.

Fossil Pleistocene herpetofaunas in Mexico, Central and South America, are barely known in comparison to North America (e.g. Holman, 1995, 2000, 2003, 2006). In Mexico, these knowledge, in turn, is scarcer in comparison with paleomammals studies, primarily focused on taxonomy (Reynoso, 2006; Tovar-Liceaga and Montellanos-Ballesteros, 2006). To date ninety fossil amphibians and reptiles have been recorded for the Pleistocene of Mexico, from which 9 are extinct and 9 have extralimital distribution (Langebartel, 1953;Brattstrom, 1955; Hibbard, 1955; Mooser-Barendum, 1958; Flannery, 1967; Álvarez and Huerta, 1975; Mooser, 1980; Van Devender *et al.*, 1985; Messing, 1986; Mead *et al.*, 2006; Reynoso and Montellano-Ballesteros, 2004; Tovar-Liceaga and Montellano-Ballesteros, 2006; Luna-Espinoza and Carbot-Chanona, 2009; Cruz *et al.*, 2010; White *et al.*, 2010;).

San Josecito Cave has been known as a highly productive paleontological locality since the earlier studies by Stock (1943). The cave faunas provide a detailed understanding of the northeastern Mexican Pleistocene vertebrates (Arroyo-Cabrales *et al*., 1989). Studies have primarily focused on mammals (Cushing, 1945; Stock 1950, 1953; Findley, 1953; Jakway, 1958; Jones, 1958; Hall, 1960; Russell, 1960; Arroyo-Cabrales *et al.*, 1993, 1996; Arroyo-Cabrales and Johnson, 1995, 2008; Esteva *et al.*, 2005), but include birds (Miller, 1943; Steadman *et al.*, 1994), lizards (Brattstrom, 1955; Mead *et al.*, 1999), and taphonomy (Arroyo-Cabrales and Johnson, 1997; Robles *et al.*, 2002; Chadefaux *et al*., 2009).

2. San Josecito Cave

San Josecito Cave (SJC) is one of the most important Pleistocene paleontological localities in México (Arroyo-Cabrales and Johnson, 2003). It is located on the western flank of the Sierra Madre Oriental, 1 km SSW from Ejido de San Josecito and 8 km SW from Arramberri (23°57'21''N, 99°54'45''O, 2250 m elevation) in northeast México (Figure 1). The cave is a single fissure with multiple entrances formed by folded Late Jurassic or Early Cretaceous limestone. Three natural recently opened entrances go down vertically from 12 to 30 m to a main cavity. All entrances provide an easy access to the cave today, although past access probably was difficult turning out the cave into a trap. The single cavity measures 34 m long and 25 m width, narrowing to the north (Arroyo-Cabrales *et al.*, 1989).

Renewed excavations were undertaken in early 1990 using a strict stratigraphic control, including the use of "taphonomic boxes" to collect microvertebrates (Arroyo-Cabrales, 1990). Radiocarbon dates assayed for the locality were the first radiometric controls for this cave, and the basis for further faunal comparisons and paleoenvironmental inferences. Ages ranged between 21 684 ± 1 168 cal BP to 46 597 ± 2 949 cal BP (Danzeglocke *et al.*, 2015) [19 740 ± 1 000 to 44 600 ± 2 500 years Ca^{14} BP; Arroyo-Cabrales *et al.* (1995)].

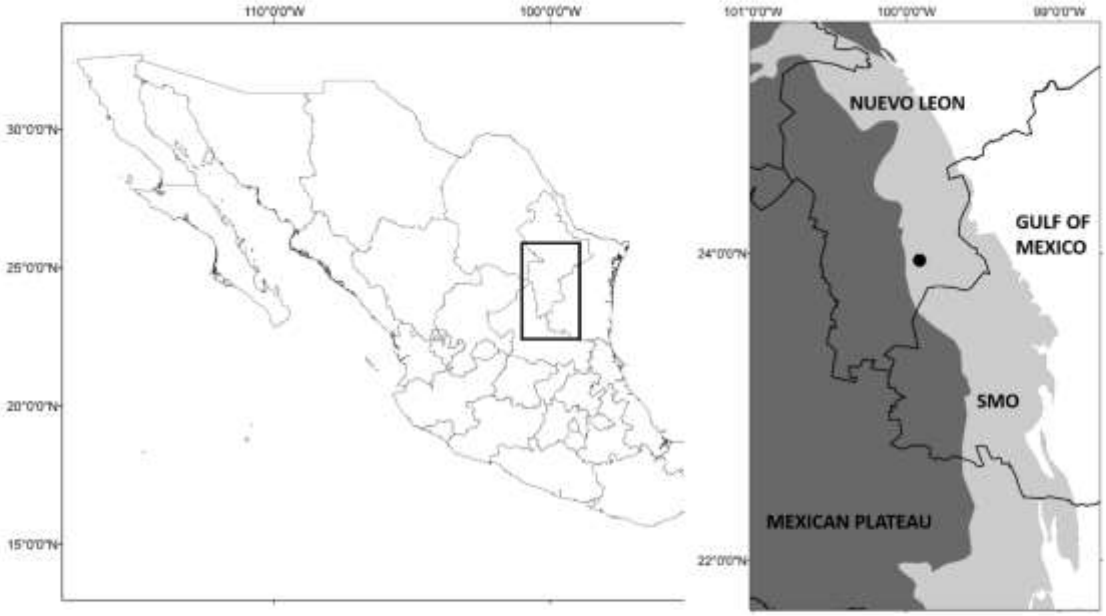

Figure 1. San Josecito Cave (black dot) located in the southern part of the State of Nuevo León, Mexico, into the Sierra Madre Oriental (SMO).

3. Material and methods

Studied material were collected from stratum 720, dated at 32673±889 cal BP (Danzeglocke *et al.*, 2015) [28005 ± 1035 años Ca^{14} BP, Arroyo-Cabrales *et al.*(1995)] indicating that squamate reptile remains were from the Late Rancholabrean North American Land Mammal Age, during the Wisconsinan glacial period (80 000–11 000 years BP) (Mead *et al.*, 1999). The bone material is on deposit in the Paleontological Collection, at the Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano", Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia (INAH) in Mexico City. Specimens were assigned catalog numbers with the acronym SJC (San Josecito Cave), and more than one element could occur per sample. Specimens were compared with recent skeletons from the Osteological Comparative Collection at the Laboratorio de Arqueozoología (DP), and the Colección Nacional de Anfibios y Reptiles (CNAR), at the Instituto de Biología, Universidad Nacional Autónoma de México. The terminology of Holman (2000) and LaDuke´s (1991) were followed for the vertebra description. Lizards' skull and dentary terminology followed Evans (2008), and osteoderms terminology that of Meszoely and Ford (1976).

3.1 Paleoenvironmental reconstruction

Diversity was quantified by calculating the total number of identifiable remains per taxon (NISP), and the minimum number of individuals (MNI), using the most frequent axial anatomical element or the most frequent paired left or right body elements (Lyman, 2008). For genera with several morphotypes, each morphotype was considered as an individual or as a taxon. Vegetation types considered were pine-oak forets (P-O), oak-pine forest (O-P), open forest and savannas (OF-S), cloud forest (CF), and decidours scrub (DS) (Table 5). Because specific taxa can inhabit one or more vegetation types, vegetation types were weighted with 1 if the species was just found in a single vegetation type, or with a ratio between 1 and 0 according to the number of environments where it can be found. Then, this value is multiplied by the NISP/NMI value (Blain *et al*., 2008). The derived value determined the habitat type for each taxon. The identified types, in turn, informed on the habitats type existing in the area during the late Pleistocene.

4. Results

4.1. Fossil squamate lizards

Squamate lizards in San Josecito Cave are the anguids *Barisia ciliaris* and *B. imbricata*, and the phrynosomatids *Phrynosoma modestum*, *P. orbiculare* and *Sceloporus.*

4.1.1. Anguidae

Barisia ciliaris is represented by 23 left maxillas (SJC 5408, 5397, 5419, 5439), 18 right maxillas (SJC 5392, 5415, 5427, 5439), and 34 osteoderms (SJC 5392, 5398, 5399, 5400, 5401, 5406, 5407, 5409, 5416, 5419, 5424, 5425, 5429, 5430, 5433-5436) (Figure 2A). Maxilla elements are important in identifying the genus *Barisia*, because they have the osteoderms preserved corresponding to preocular, cantholoreal and postnasal scales. Two cantholoreals or one cantholoreal not exceeding the preocular and postnasal scales, allowing separation of the fossil maxillas from *B. jonesi*, *B. imbricata*, *B. planifrons* and *B. levicollis*. In these four species, a single cantholoreal contact one or two supralabials, exceeding the preocular and the postnasal scales (Guillette and Smith, 1982). Two cantholoreal scales are present in *B. ciliaris* and *B. herrerae*, but in

B. ciliaris, they are vertical in contrast to that in *B. herrerae* with horizontal scales (Zaldívar-Riverón and Nieto-Montes de Oca, 2002).

Oblique keeled osteoderms in the fossil material strengthened the identification as *Barisia ciliaris. B.levicollis* and *B. planifrons* also have oblique keel osteoderms (Guillette and Smith, 1982). As no maxillas similar to these species were found, their presence at SJC is unlikely.

Mead *et al*. (1999) identified the fossil material from SJC as *Barisia* cf. *B. imbricata*. In the 1990's the species *B. imbricata* consisted of four subspecies *B. imbricata ciliaris, B. imbricata imbricata, B. imbricata jonesi,* and *B. imbricata planifrons*, that later were raised to specific level (Smith *et al.*, 2002).

Barisia ciliaris is distributed today in the Sierra Madre Oriental that includes the SJC region, the Sierra Madre Occidental, and the Mexican Central Plateau (Zaldívar-Riveron *et al*., 2005). This species inhabits pine and pine-oak forest (Guillette and Smith, 1982), and *Pinus* forest and savanna in the State of Nuevo León, between 3200-3300 m elevations (Guillette and Smith, 1982; Contreras-Lozano *et al.*, 2011, 2012).

The alligator lizard *Barisia imbricata* is represented by eight right maxillas (SJC 5439), four left maxillars (SJC 5439) and 20 osteoderms (SJC 5403, 5421, 5400, 5405, 5417, 5419, 5416, 5392, 5424, 5423, 5426, 5390) (Figure 2B). Maxillas have a single enlarged, broad-based cantholoreal scale that touches two supralabials scales that allows a separation from *B. ciliaris* and *B. herrerae*, that have two cantholoreals. Obtuse keels in osteoderms allow the exclusion of the fossil material from *B. planifrons* and *B. ciliaris* (Guillette and Smith, 1982). The combination of a single enarged cantholoreal with obtuse keels in osteoderms indicates that the fossil material belongs to *B. imbricata*.

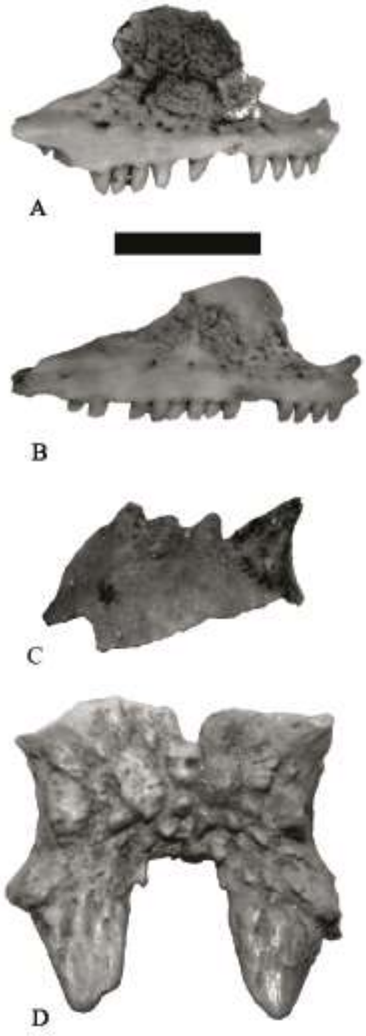

Figure 2. Fossils lizard remains recovered from San Josecito Cave. A, *Barisia ciliaris* (SJC 222311) right maxilla. B, *Barisia imbricata* (SJC 222311) right maxilla. C, *Phrynosoma modestum* (SJC 5406) left squamosal. D, *Phrynosoma orbiculare* (SJC 222311) parietal bone. A and B in labial view; C and D in dorsal view. Bar = 50 mm.

B. imbricata occurs today along the Transvolcanic Belt and adjacent regions (Zaldívar-Riveron *et al*., 2005). This species inhabits pine, pine-oak and oak forests (Guillette and Smith, 1982). This species does not occur in the State of Nuevo León today.

While *Barisia imbricata* and *B. ciliaris* now are considered different species, their biogeographic boundaries are difficult to define (Guillette and Smith, 1982; Zaldívar-Riveron *et al*., 2005). *Barisia ciliaris* and *B. imbricate* are sympatric in the State of Hidalgo (Guillette and Smith, 1982; Zaldívar-Riveron *et al.*, 2005). Both species were sympatric in SJC during the Pleistocene indicating that sympatry extended as far as 450 km north to the State of Nuevo León.

4.1.2. Phrynosomatidae

The horned lizard *Phrynosoma modestum* is represented by a left squamosal (SJC 5406) (Figure 2C). The squamosal has four temporal horns with the most posterior one taller and wider than the others. The horns are oriented horizontally with the two posterior horns bended gently upward. Among horned lizards the squamosal of *P. taurus* has a large temporal horn. *Phrynosoma asio* and *P. cerroense* have two temporal horns, and *P. boucardii*, *P. braconnieri, P. cornutum, P. coronatum, P. ditmarsi, P douglassii, P. m'callii, P. orbiculare* and *P. platyrhinos* have three temporal horns. *Phrynosoma solare*, *P. modestum,* and *P. josecitensis* are the only ones with four horns (Brattstrom, 1955; Presch 1969) as the fossil material. *Phrynosoma modestum* differs from *P. solare* and *P. josecitensis* in that the one latter temporal horn is larger than the rest, while in the other two species the two latter temporal horns are larger than the rest (Brattstrom, 1955; Presch 1969; Montanucci, 1987).

Phrynosoma modestum is found from West Texas, southern New Mexico and southeastern Arizona to Central Mexico. This species inhabits open shrub areas in arid and semiarid watersheds (Sherbrooke, 2003). It occurs today in *Juniperus* forest in the State of Nuevo León, between 600-1250 m elevation (Canseco-Márquez *et al.*, 2004; Lazcano *et al.*, 2007), but its distribution range does not extends into the SJC area.

The horned lizard *Phrynosoma orbiculare* is represented by one right dentary (SJC5439), two left dentaries (SJC5439), one frontal bone (SJC 5439), one parietal bone (SJC 5439) and one right parietal horn (SJC 5439) (Figure 2D). The dentary is convex labially with a flat ventral margin, typical of *Phrynosoma* (Mead *et al.*, 1999). The Meckelian canal is closed in the middle as in *P. bracconnieri, P. coronatum, P. douglassii, P. orbiculare* and *P. solare* (Presch, 1969; Montanucci, 1987). *Prhynosoma solare* has dentary horns, a character absent in the fossil material. The ratio between the number of teeth and the length of the tooth row rules out fossil dentaries as *P. bracconnieri* (Table 1).

Table 1. Ratios between dentary number teeth (nt) and dentary length teeth row (ltr) to diferent species of *Phrynosoma*, provided by Mountanucci (1989), Meyer *et al.* (2006), osteological reference material (DP), and fossil material (SJC). ND, no data.

Source	Taxon	nt/ltr (mm)
SJC 5439	*P. orbiculare* fossil	2.09
SJC 5439	*P. orbiculare* fossil	1.88
SJC 5439	*P. orbiculare* fossil	ND
Montanucci, 1989	*P. braconnieri*	3.26
Montanucci, 1989	*P. coronatum*	2.19
Montanucci, 1989	*P. douglassi*	2.09
Montanucci, 1989	*P. orbiculare*	2.81
Meyer *et al.,* 2006	*P. braconnieri*	3.47
Meyer *et al.,* 2006	*P. coronatum*	2.89
Meyer *et al.,* 2006	*P. orbiculare*	2.32
DP 8182	*P. orbiculare*	2.56
DP 8146	*P. orbiculare*	2.84

The frontal bone is flat and the ciliar horns are extended horizontally as in *Phrynosoma douglassii* and *P. orbiculare* (Presch, 1969). The parietal bone is the most diagnostic among all remains. Contrary to *P. douglassii* that lack horns on the parietals, the fossil specimens have two parietal horns that are strong. The extra ornamentations are pointed as those of *P. orbiculare* and *P. braconnieri*, but they are not elongated like spines as in *P. coronatum*, *P. cornotum* and *P. solare* (Montanucci, 1987).

The length of parietal horns of the fossil material has been compared with data from Montanucci (1987) and osteological material as shown in Table 2. The length of the parietal horns in the fossils are similar to those of *Phrynosoma asio*, *P. braconnieri* and *P. orbiculare*. The ornamentation surface, however, has low rugose tuberosities that are present in *P. braconnieri* and *P. orbiculare* but not in *P. asio.* The ratio between the tooth number and tooth row length distinguish *P. braconnieri* from *P. orbiculare* (Table 1).

The fossil material was identified as *Phrynosoma orbiculare* according to the following combination of characters: meckelian groove close-fitting to the middle-line, without horns or ornamentations in the labial side of dentary, frontal bone flat with tapered tubers, and ratio between the parietal horns length and skull length between 3.03-5.02 mm.

Table 2**.** Parietal horns length of different species of *Phrynosoma* provided by Montanucci (1989), osteological reference material (DP), and fossil material (SJC).

Source	Taxon	Parietal horns length (mm)
SJC 222311	*Phrynosoma orbiculare* fossil	4.1
SJC 222311	*Phrynosoma orbiculare* fossil	4.3
Montanucci, 1989	*Phrynosoma asio*	3.60-5.97
Montanucci, 1989	*Phrynosoma braconnieri*	2.55-4.22
Montanucci, 1989	*Phrynosoma cornutum*	5.96-9.49
Montanucci, 1989	*Phrynosoma coronatum*	6.48-10.32
Montanucci, 1989	*Phrynosoma ditmarsi*	1.11-1.80
Montanucci, 1989	*Phrynosoma mcallii*	9.11-9.92
Montanucci, 1989	*Phrynosoma modestum*	2.19-3.63
Montanucci, 1989	*Phrynosoma orbiculare*	3.03-5.02
Montanucci, 1989	*Phrynosoma platyrhinos*	5.14-6.39
Montanucci, 1989	*Phrynosoma solare*	7.48-11.92
Montanucci, 1989	*Phrynosoma taurus*	1.86-3.09
DP 8182	*Phrynosoma orbiculare*	5.1
DP 8146	*Phrynosoma orbiculare*	4

Phrynosoma orbiculare is endemic to Mexico, found in the Sierra Madre Oriental, Sierra Madre Occidental, and Mexican Plateau. This species inhabits the semiarid shrub and pine and oak mountain forests (Sherbrooke, 2003).

The spiny lizards *Sceloporus* is represented by four left dentaries (SJC 5391, 5397, 5412, 5432), one right dentary (SJC 5418), four right maxillas (SJC 5402, 5414, 5416, 5426), three left maxillas (SJC 5391, 5406, 5421), and two premaxillas (SJC 5393, 5434). Teeth with tricuspid and chisel like crowns are typical for *Sceloporus* (Etheridge, 1964). Althought the fossil specimens were compared with some *Sceloporus* species, the high diversity and variability within the genus (Etheridge, 1964) prevents separation of the remains to the species level. The fossil specimens have different features that distinguish them from each other, suggesting the presence of more than one species as suggested by Mead *et al*. (1999).

Sceloporus is the most diverse lizard genus of North and Central America with 91 known species (Bell *et al*., 2003). They occur from southern Canada to Panama (Wiens and Reeder, 1997), in a wide variety of environments from the beach to the coniferous forests.

4.2. Fossil squamate snakes

The fossil snakes from San Josecito Cave included the taxa *Heterodon simus*, *Hypsiglena*, *Storeria*, *Tantilla* and *Crotalus*.

4.2.1. Colubridae

The hognose snake *Heterodon simus* is represented by one cervical vertebra (SJC 5439) (Figure 3A1-2.). The vertebra is identified as *Heterodon* for the following reasons: its strongly depressed neural arch and without subcentral bridges (Meyland, 1982); the neural spine is longer than high with the anterior margin concave and posterior margin convex; and different from *Farancia* it has two concave margins present (Holman, 2000). Meyland (1982) has separated morphologically the *Heterodon* species using a discriminant analysis (Table 3). Based on Meyland (1982) results, the fossil vertebra matches *H. simus.*

Table 3**.** Different vertebra ratios for *Heterodon* species provided by Meyland (1982) and fossil material (SJC). Abbreviations: cl, centrum length; naw, neural arch width; po-pr, postzygapophysis to prezygapophysis length; pr-pr, prezygapophysis to prexygapophysis width; zw, zygosphene width. Measured in mm, mean ± standar deviation.

Source	Taxon	po-pr/naw	cl/naw	pr-pr/cl	pr-pr/zw
SJC 222311	*H. simus* fossil	1.22	1.07	1.5	2.75
Meyland, 1982	*H. nasicus* recent	1.59±0.130	1.68±0.20	1.40±0.12	2.35±0.18
Meyland, 1982	*H. nasicus* fossil	1.62±0.17	1.70±0.19	1.40±0.11	2.37±0.23
Meyland, 1982	*H. platyrhinos* recent	1.72±0.16	1.57±0.17	1.41±0.08	2.20±0.18
Meyland, 1982	*H. platyrhinos* fossil	1.75±0.17	1.62±0.15	1.39±0.11	2.23±0.16
Meyland, 1982	*H. simus* recent	1.33±0.08	1.56±0.15	1.49±0.14	2.30±0.12

The Southern Hognose Snake *Heterodon simus* ranges throughout the southeastern United States from southern North Carolina to southern Florida extending west along the Gulf of Mexico to southern Louisiana. It inhabits xeric environments and highlands, preferring sandy soils in *Pinus* forests and low and open underwood (Jordan, 1998). The SJC occurrance is the first record of *Heterodon* for the Pleistocene of Mexico and the first record of *H. simus* in Mexico.

Hypsiglena is represented by six trunk vertebrae (SJC 5409, 5410, 5412, 5414, 5431, 5435) (Figure 3C1-4). The vertebrae are identified as *Hypsiglena* based on their longer than wider centrum with a length between 1.85 to 2.4 mm; depressed neural arch in posterior view, short neural spine, and posteriorly oriented accessory process (Van Devender and Mead, 1978); well developed interzigapophisial bridges and lack of anterior projections on the neural spine (LaDuke, 1991).

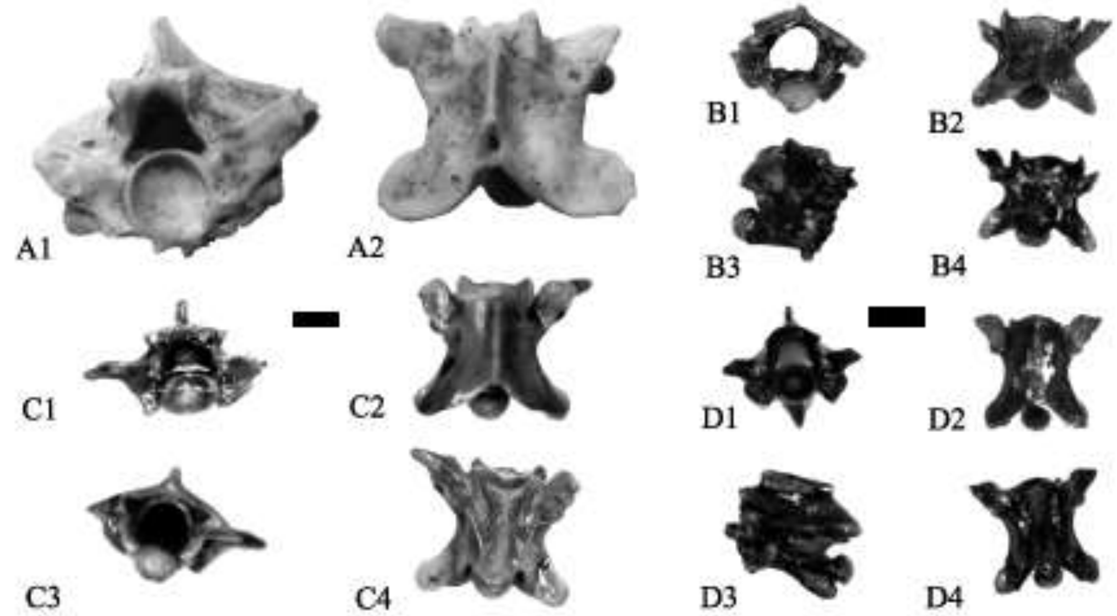

Figure 3. Fossil snake vertebrae recovered in San Josecito Cave. A, *Heterodon simus* (SJC 222311) cervical vertebra. B, *Tantilla* (SJC 5435) trunk vertebra. C, *Hypsiglena* (SJC 5412) trunk vertebra. D, *Storeria* (SJC 5398) trunk vertebra. A1, C1 and D1 in anterior view; A2, B2, C2 and D2 in dorsal view; B1 and C3 in posterior view; B3 and D3 in lateral view; B4, C4 and D4 in ventral view. Left bar = 1 mm. Right bar = 0.5 mm.

The *Hypsiglena torquata* complex is composed by seven species *H. torquata*, *H. affinis*, *H. slevini, H. tanzeri, H. jani, H. chlorophacea* and *H. ochrorhyncha* (Mulcahy, 2008). The fossil material cannot be separated at the species level because useful quantitative or qualitative features that would separated them could not be identified. *Hypsiglena* is distributed from Western and Central United States to the Balsas Depression and the Mexican Plateau (Mulcahy, 2008). *Hypsiglena jani* occurs today in the State of Nuevo León (Lazcano *et al.*, 2007).

The Mexican Brown snake *Storeria* is represented by16 cervical vertebrae (SJC 5391, 5392, 5402, 5410-5412, 5414, 5431) and 45 trunk vertebrae (SJC 5391-5393, 5395, 5398, 5399, 5401, 5402, 5408-5412, 5414, 5416, 5431, 5432, 5437)(Figure 3D1-4.). The fossil remains are identified as *Storeria* based on their small size with a centrum length of 1.1-1.95 mm; low neural spine with concave margins (Auffenberg, 1963); small, posteriorly directed hypaphophysis; and the neural spine extending beyond the neural arch posteriorly in dorsal view (Holman, 2000). The four species of genus *Storeria* today are: *S. dekayi*, *S. hidalgoensis*, *S. occipitomaculata* and *S. storerioides* (Linner and Casas-Andreu, 2008). Auffenberg (1963) provides quantitative data to discriminate *S. dekayi* and *S. occipitomaculata* vertebrae; and *S. storerioides* data were added. The results separate the fossil vertebrae from *S. dekayi*, but not from other species (Table 4).

Table 4. Different vertebra ratios for *Storeria* species provided by Auffenberg (1963), osteological reference material (CNAR), and fossil material (SJC).). cl, centrum length. naw, neural arch width. nlu, length at the dorsal edge of neural spine. hn, height of neural spine. po-pr, postzygapophysis to prezygapophysis length. pr-pr, prezygapophysis to prezygapophysis width. zw, zygosphen width.

Source	Taxon	cl/naw	po-pr/pr-pr	nlu/zw	nlu/hn
SJC 5391-5437	*Storeria* fossil	1.66±0.112	0.989±0.04	1.178±0.111	2.881±0.909
CNAR uncatalogued	*S. storerioides*	2.19±0.069	1.084±0.026	1.13±0.018	3.193±0.279
Auffenberg 1963	*S. dekayi*	1.98±0.169	1.165±0.078	1.295±0.092	3.445±0.304
Auffenberg 1963	*S. occipitomaculata*	1.89±0.113	1.075±0.035	1.62±0.028	5.27±0.382

Storeria is widely distributed in North America, from northeastern Canada, eastern United States, Mexico to Honduras. It is found between 635 to 3200 m elevation in coniferous forests (Trapido, 1944). Today, *S. dekayi texana* (Contreras-Lozano *et al.*, 2010) and *S. hidalgoensis* (Lazcano *et al.*, 2009a, 2009b) range in the State of Nuevo Leon.

The black-headed snake *Tantilla* is represented by one cervical vertebra (SJC 5435) and two trunk vertebrae (SJC 5425, 5435) (Figure 3B1-4.). The fossil vertebrae are identified as *Tantilla* based on a centrum length less than 1.75 mm, subcentral bridge absent, short accesory process and low neural spine (Meyland, 1982); hemal keel gladiate; parapophysis like a small projection; convex zygosphene in dorsal and anterior view (Auffenberg, 1963); and shallow neural arch (LaDuke, 1991; Holman, 2000).

The genus *Tantilla* today is composed of 53 species (Wilson, 1999). They are distributed from the southern United States to Argentina (Holman, 2000). In Mexico, 27species are known and 11 in the United States. Three species are found around the SJC area today: *T. atriceps, T. rubra,* and *T. wilcoxi* (Lazcano *et al.*, 2007). The genus is present in different vegetation types and widely distributed.

4.2.2. Viperidae

The rattlesnakes *Crotalus* is represented by 41 trunk vertebrae (SJC 5388, 5391-5393, 5396, 5397, 5405, 5407, 5409, 5410, 5412, 5419, 5422, 5423, 5425, 5432, 5436, 5439). The fossil specimens are identified as *Crotalus* based on the hypapophysis almost as wide as the condyle; large paracotilar foraminae; and epizygapophysial spines absent. These features allow separation of the fossil material from *Agkistrodon.* Subcentral bridges, a tiny anterior processes, and neural spine are absent. These absences allow the separation of the fossil material from *Sistrurus* (Auffenberg, 1963; Holman, 1981; LaDuke, 1991; Meyland, 1982). Today, *Crotalus* is composed of 41 species (Campbell and Flores-Villela, 2008; Uetz and Hallermann, 2015). It is not possible to separate the species by vertebral morphology (Parmley, 1990).

Crotalus is distributed from southern Canada to northern Argentina, excluding the Amazon Basin tropical forest (Holman, 2000). They inhabit different environments from desert to coniferous forests (Murphy *et al.*, 2002). Six species are found today in the State of Nuevo León; *C. atrox*, *C. lepidus, C. pricei, C. molossus, C. scutulatus,* and *C. totonacus* (Lazcano *et al.*, 2007, 2009a, 2009b; Contreras-Lozano *et al.*, 2010).

4.3. Extralimital taxa

Of the 10 fossil herpetofauna identified taxa, three do not occur in the SJC region today. In the late Pleistocene, the squamate diversity in SJC was composed of elements from different today´s biogegraphical regions: 1) *Heterodon simus* from eastern United States, 2) *Barisia imbricata* from the Neovolcanic Transmexican Belt; and 3) *Phrynosoma modestum* from the Mexican Plateau (Figure 4).

4.4. Paleoenvironment

The Habitat Weighted analysis for each taxon was based on the dominant vegetation found today in the localities where the different taxa are distributed. Results indicated that vegetation in the SJC surroundings was an open temperate forest, grassland, and oak-pine forest, during the Late

Pleistocene (Table 5). *Phrynosoma modestum* was the only taxon that inhabits xerophylous scrub (Figure 5) and *Juniperus* forest.

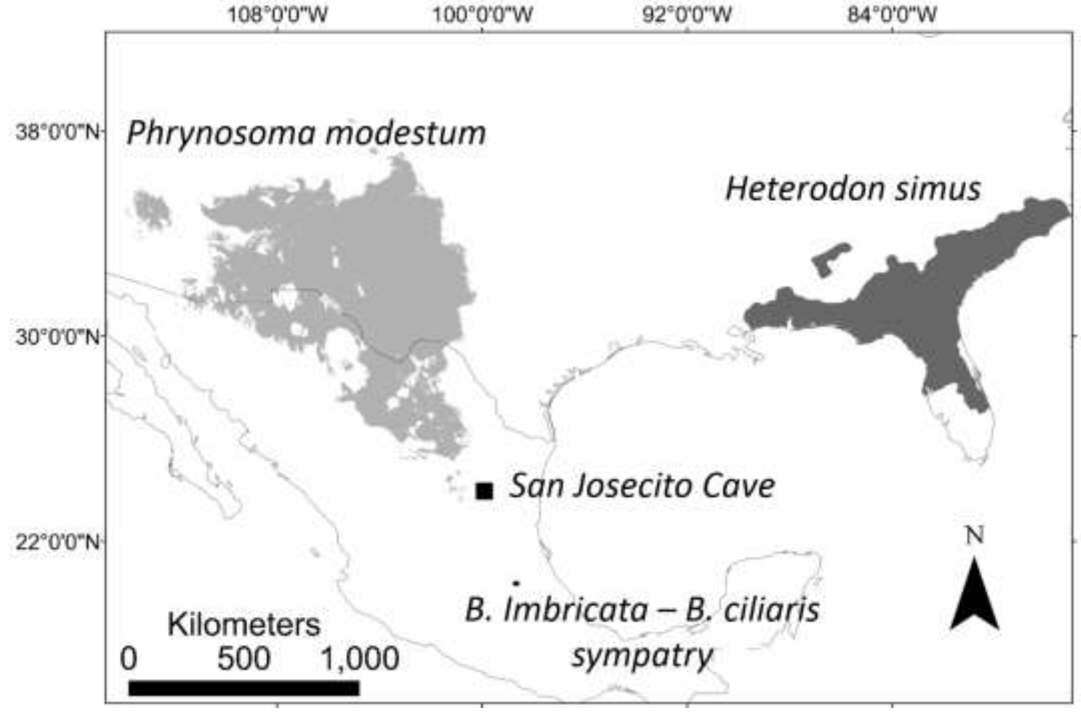

Figure 4. Recent distributional range of fossil herpetofauna taxa identified from San Josecito Cave (Black square), indicating relationship of Sierra Madre Oriental (San Josecito Cave) with eastern North America (*Heterodon simus*), Mexican Plateau (*Phrynosoma modestum*) and Trans Volcanic Belt (*Barisia imbricata-Barisia ciliaris* sympatry area).

5. Discussion

5.1 Pleistocene Squamata

The SJC squamate reptile diversity has increased its fossil record to 11 taxa of four families, eight genera, and five reptiles species, including seven new records (Brattstrom, 1955; Mead *et al.*, 1999) (Table 6). This locality contains a relatively large number of taxa, exceeded only by Santa Cruz Nuevo in Puebla (Tovar-Liceaga and Montellano-Ballesteros, 2006) and Rancho La Brisca in Sonora (Van Devender *et al.*, 1985). *Heterodon simus* represents the first record of the species in Mexico. *Barisia ciliaris*, *Phrynosoma modestum, Heterodon simus*, *Tantilla*, and *Storeria* are the first records for the Pleistocene in Mexico; and *Barisia imbricata* is first record for the State of Nuevo León. As noted by Mead *et* al. (1999), no specimens have been identified as the extinct species *Phrynosoma josecitensis* by Brattstrom (1955).

Table 5. Taxa abundance and weighted habitat for the San Josecito Cave squamate reptile assemblage. NISP, number of identifiable bones. MNI, minimum number of individuals. P-O, Pine-Oak forest. O-P, Oak-Pine forest. CF, Cloud forest. DS, Desert Scrub. OF-S, Open forest and Savannah.

Taxa	Abundance			Vegetation type				
	NISP	MNI	NISP/MNI	P-O	O-P	CF	DS	OF-S
Barisia ciliaris	41	23	1.78	0	0.89	0	0	0.89
Barisia imbricata	12	8	1.5	0.75	0	0	0	0.75
Phrynosoma orbiculare	5	2	2.5	0.62	0.62	0	0.62	0.62
Phrynosoma modestum	1	1	1	0	0	0	0.5	0.5
Sceloporus	14	4	3.5	0.7	0.7	0.7	0.7	0.7
Tantilla	3	1	3	0.75	0.75	0.75	0.75	0
Heterodon simus	1	1	1	0.5	0	0	0	0.5
Hypsiglena	6	1	6	1.5	1.5	0	1.5	1.5
Storeria	61	6	10.17	3.36	3.36	0	0	3.36
Crotalus	41	4	10.25	2.05	2.05	2.05	2.05	2.05
Total				10.23	9.87	3.5	6.12	10.87

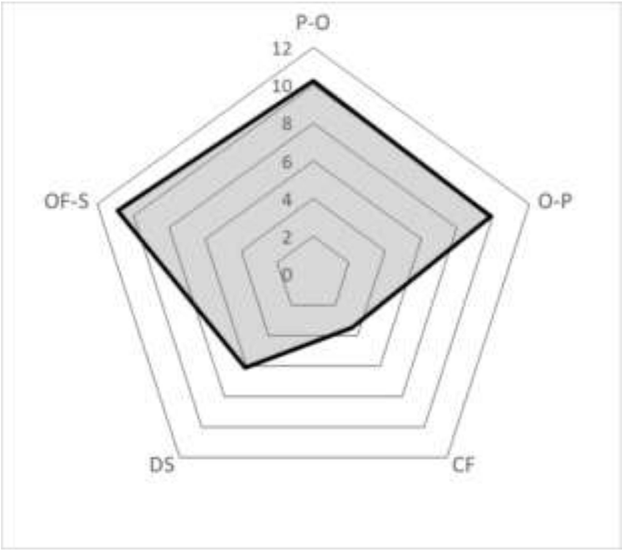

Figure 5**.** Palaeoenvironmental reconstruction using the Habitat Weighted analysis for the squamate reptiles assemblage of San Josecito Cave area for the late Pleistocene. The highest value is with OF-S and P-O, indicating a mosaic vegetation including open forest of *Pinus*-*Quercus* with grassland. Numbers are of habitat weighted values. P-O, Pine-Oak forest. O-P, Oak-Pine forest. CF, Cloud forest. DS, Desert Scrub. OF-S, Open forest and Savannah.

Table 6. Late Pleistocene squamate reptiles from San Josecito Cave

Brattstrom 1955	Mead *et al.* 1999	Present study
Squamata	Squamata	Squamata
	Anguidae	Anguidae
	Barisia cf. *B. imbricata*	*Barisia imbricata*
		Barisia ciliaris
Phrynosomatidae	Phrynosomatidae	Phrynosomatidae
Phrynosoma josecitensis †		
Phrynosoma orbiculare	*Phrynosoma* cf. *orbiculare*	*Phrynosoma modestum*
	Sceloporus spp.	*Phrynosoma orbiculare*
		Sceloporus spp.
		Colubridae
		Tantilla sp.
		Heterodon simus
		Hypsiglena
		Storeria sp.
		Viperidae
		Crotalus spp.

5.2 Paleodistribution

An abrupt retraction occurs in the distribution of *Heterodon simus* from the Sierra Madre Oriental to the eastern United States. Some mammals, like the Southern bog lemming *Synaptomys cooperi* and the Meadow vole *Microtus pennsylvanicus* follow the same retraction pattern (Ceballos *et al.*, 2010; Ferrusquía-Villafranca *et al.*, 2010).

Barisia imbricata also shows a change in its distribution to the Mexican Transvolcanic Belt. The association between the Sierra Madre Oriental and the Mexican Transvolcanic Belt have not been discussed for mammals in similar studies (e.g. Ceballos *et al.*, 2010; Ferrusquía-Villafranca *et al.*, 2010). Molecular data for *Ambystoma*, *Crotalus,* and *Phrynosoma* indicate a strong phylogenetic relation between the Mexican Transvolcanic Belt and the Sierra Madre Oriental (Shaffer and McKnight, 1996; Bryson *et al.*, 2011, 2012). The presence of *Barisia imbricata* and *B. ciliaris* in the same geographic area has also been recognized in the State of Hidalgo (Guillette and Smith, 1982; Zaldívar-Riverón *et al.*, 2005). This co-occurance indicates that sympatry extended as far as 450 km north to the State of Nuevo León during the Pleistocene.

Although *Phrynosoma modestum* is found in the State of Nuevo León, it does not inhabit the pine-oak forest around SJC. It inhabits the open shrub areas in arid and semiarid watersheds (Sherbrooke, 2003), and *Juniperus* forest in the State of Nuevo León (Canseco-Márquez *et al.*, 2004; Lazcano *et al.*, 2007). The distributional pattern linking the Sierra Madre Oriental with the Mexican

Plateau represent by *P. modestum* is also repeated by the spiny pocket mouse *Liomys irroratus* (Ceballos *et al.*, 2010; Ferrusquía-Villafranca *et al.*, 2010). This relationship supports the proposal of Martin (1958), that a strong connection existed between those two areas during the Pleistocene. This suggestion is based on biogeographic analysis of amphibians and reptiles, climate, vegetation types and historical geology in the Gómez Farías Region, Tamaulipas. This pattern is also inferred for the genus *Sceloporus poinsettii* (Gadsden *et al.*, 2005) y *S. mucronatus* (Méndez-de la Cruz *et al.*, 1994).

Shifts in taxa distribution appear related to environmental changes associated with changes in global climate (Polly *et al.*, 2011). During the Pleistocene, climate and environmental conditions were highly dynamic. Distributional changes found in studies such as phylogeography, show the expansion and contraction of amphibian and reptiles ranges during glacial and interglacials (Douglas *et al.*, 2006, 2009; Hutchison *et al.*, 1999; McGuire *et al.*, 2007; Waltari *et al.*, 2007). We suggest that in the past climatic and environmental condition necesary to shelter the presence of *H. simus*, *B. imbricata* and *P. modestum* was present, although these species are not together today.

5.3 Paleoenvironment

In the SJC area during the late Pleistocene the vegetation is a mosaic principally of an open forest with savanna, dominated by *Pinus* and *Quercus*, and xeric scrub with *Juniperus*. This reconstruction differs from previous environmental inferences for the SJC area based on mammals (Arroyo-Cabrales *et al.*, 1989, 1993; Arroyo-Cabrales and Johnson, 1995, 1997), birds (Steadman *et al.*, 1994), and lizards (Mead *et al.*, 1999). Those studies suggest the presence of oak-pine forest similar to the current setting. Our data expanded palaeoenvironmental reconstruction in agreement with pollen data recovered from the Pleistocene in the northern portion of Mexico. Those data indicates that *Juniperus* forest into the xeric scrub was widely spread in the late Pleistocene. This forest type around SJC is 400 km south from its current distribution (Caballero *et al.*, 2010; Metcalfe, 2000, 2006; Van Devender and Mead, 1978).

The presence of two *Barisia* species in the same geographic area is uncommon. Today, *B. ciliaris* and *B. imbricata* are sympatric only in Atotonilco el Grande (Figure 4), northern State of Hidalgo (Guillette and Smith, 1982; Zaldívar-Riverón *et al.*, 2005). Assuming niche conservatism, the weather conditions in SJC area, 450 km north, would have been similar during the Pleistocene. Data from 1951 to 2010 in the Atotonilco el Grande weather station show an annual mean temperature of 16.3°C, and an annual precipitation of 787.3 mm (smn.cna.gob.mx). In contrast, San Francisco (the closest weather station to the cave area), has an annual mean temperature of 17.3°C and annual precipitation of 319.9 mm (smn.cna.gob.mx). During the Pleistocene, then, the annual mean temperature in the SJC area may have been 1°C lower and the annual precipitation 467.4mm greater than today. These conditions also allowed the presence of other temperate climates taxa like *Marmota* and *Synaptomys* (Davis, 2005; Ceballos *et al.*, 2010).

6. Conclusions

Results from this study indicate the herpetological community has varied from late Pleistocene to present in the SJC area. Changes in squamate reptiles' distribution showed a strong relationship between the Sierra Madre Oriental with the eastern United States, Mexican Transvolcanic Belt, and Mexican Plateau. Ranges contracted to the north or south of the cave area. During the late Pleistocene, the SJC area had a mosaic vegetation composed principally of an open forest with grasslands dominated by *Pinus* and *Quercus*, and a secondary xeric scrub with *Juniperus.* The annual mean temperature in SJC area appears to have been 1°C lower and the annual precipitation 467.4mm greater than today. This inference is based the sympatric distribution between *Barisia imbricata* and *B. ciliaris.*

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CAPÍTULO III

EFECTO DEL CAMBIO CLIMÁTICO Y ESTRUCTURA DE LA VEGETACIÓN EN LOS ANFIBIOS Y REPTILES DEL CUARTERNARIO

(*Quaternary Research:* Enviado*)*

Effect of the climate changes and vegetation structure in amphibians and reptiles of the Quaternary

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Abstract

Climate and ecological changes during the Quaternary modified the structure of biological communities through time. Based on the herpetofauna of the Sonoran Desert we reconstructed the late Quaternary paleoclimate and vegetation structure estimating changes in the amphibian and reptile communities through time. Of the total of fossil herpetofauna, two species of anuran, four of lizards, three of snakes and two of turtles are not found nowadays in the Sonoran Desert. Compared with current climate data, we found an important decrease in temperature and an increase of precipitation during the mid-Holocene, the Younger Dryas and the early Wisconsinian. The early Holocene, the Pleistocene-Holocene transition, the Allerød/Bølling and the Last Glacial Maximum presented drier conditions than recent. Vegetation structure in stripes, as found today, featured in the mid-Holocene and early Wisconsinian. In contrast, from the early Holocene up to the Last Glacial Maximum the vegetation structure was in mosaic. The amphibian and reptile communities are first affected by changes in vegetation structure and then by climate changes.

Key words

Amphibian and reptile communities; Pleistocene-Holocene; Paleoclimate; Vegetation structure.

Introduction

Lacustrine records provide the most used and reliable data to reconstruct paleoclimate and paleoenvironment of past biological communities because of their depth temporal resolution (Hodell *et al.*, 2008). Most studies in these sites are based on pollen information and have shown that past communities are not always analogous with recent ones (*e.g.* McAuliffe and Van Devender, 1998; Jackson and Overpeck, 2000; Hodell *et al.*, 2008; Gonzales *et al.*, 2009; Correa-Metrio *et al.*, 2012). This same pattern has been found during the late Quaternary research in studies based on fossil fauna (Stewart, 2009). For example, in North America mastofauna that characterize eastern United States today was absent during the late glacial (Semken Jr. *et al.,* 2010); and according to the vegetation reconstruction made by Jackson and Overpeck (2000), the mammal communities indicated a combination of deciduous forest, grassland, subtropical savannah and boreal elements in the southeastern region of North America (Semken Jr. *et al.,* 2010). Evidences of non-analogous communities between glaciations and interglaciations in the Holocene and Pleistocene were described with fossil mastofauna in Great Britain, aevidencing that faunas are more disparate faunas according to the increment of time in which they are compared (Stewart, 2008).

Biological communities are structured according to how species respond to climate changes in the World (Stewart, 2009), for how long those changes occur, and the magnitude and direction of the response of each taxon. It is predicted that communities do not have to react as unique entities, instead they respond to the individual reaction of each species to climate and environmental changes (Jackson and Overpeck, 2000. This forms communities with different structures and composition between a time range interval (Stewart and Cooper, 2008).

Herbivorous megafauna (mammals ≥44kg) promoted spatial heterogeneity forming vegetation mosaics in the same zone, combining open vegetation and woody zones with a great diversity of habitats and species (Guthrie, 1984). The extinction of the megafauna caused a decrease in the interaction between large herbivores and vegetation, changing the influence of the CO_2 in the nitrogen cycle and plant nutritional contents, while fires incidence increased because of the accumulation of plant material (Johnson, 2009a). The megafauna extinction along with different climate conditions thereafter defined the Pleistocene-Holocene transition, allowing the restructuration of vegetal communities in altitudinal and latitudinal stripes, during the Holocene (Johnson, 2009a, 2009b; Gill *et al.*, 2009, 2012, 2014; Faith, 2011, 2014; Yansa and Adams, 2012; Brault *et al.*, 2013; Yeakel *et al.*, 2013; Froyd *et al.*, 2014; Weigl and Knowles, 2014). Changes in vegetal communities structure should be also reflected in the composition of the other smaller and more habitat-dependent vertebrate communities.

Fossils of micromammals, birds, amphibians, reptiles and fish show important features for past climates and environment reconstruction (Holman, 1995; Legendre *et al.*, 2005; Blain *et al.*, 2008, 2009, 2010, 2011, 2012, 2013; Corona-M., 2008). The specialization of amphibians and reptiles to certain environments allows the reconstruction of past climates making them excellent markers in sites with fossils remains of these groups (Blain *et al.*, 2008, 2009, 2010, 2011, 2014).

In this study, we analyzed Pleistocene and Holocene amphibians and reptiles to answer the following question: Does changes in the structure of amphibian and reptile communities during the Quaternary respond to the climate change or to the vegetation structure type?

Material and methods

Study site

The sites with fossil amphibians and reptiles in the Sonoran Desert used in this study are Whipple Mountains, Redtail Peaks, Artillery Mountains, New Water Mountains, Burro Canyon and Brass Cap Point, Wellton Hills, Wolcott Peak, Tucson Montains (Van Devender and Mead, 1978), and Rancho la Brisca (Van Devender *et al.*, 1985) (Figure 1, Table 1). The Sonoran Desert is a subtropical arid area largely located in the peninsula of Baja California, western Sonora, southwestern Arizona and southeastern California. Main vegetation type in the Sonoran Desert is xerophytic scrub (Rzedowski, 2006) with arboreal cacti, wich reflects a strong affinity with the subtropical thorn scrub found in the south of the Sonoran Desert (Van Devender, 1990). It has elevations from below sea level up to 1000 m. The annual mean mid-temperature ranges between 12 to 26°C and mean annual diurnal range of 20°C. In summer, temperatures can reach more than 40°C in shade in 74.2% of the Sonoran Desert area. Highest temperatures occur in June or July, with a second maximum during

September, typical for intertropical zones. The temperatures can be cold at night, although the intensity and frequency of low temperatures diminish towards the south. Mean annual precipitation is lower than 100 mm. Rainy seasons occur twice a year with strong monsoons in summer for Sonora and Arizona and in winter for Baja California Peninsula. The high pressure semi-permanent Northeast Pacific wind cell and the water cold current of the California Gulf causes, arid or semi-arid climates in 95% of the Sonora surface (Brito-Castillo *et al.*, 2010).

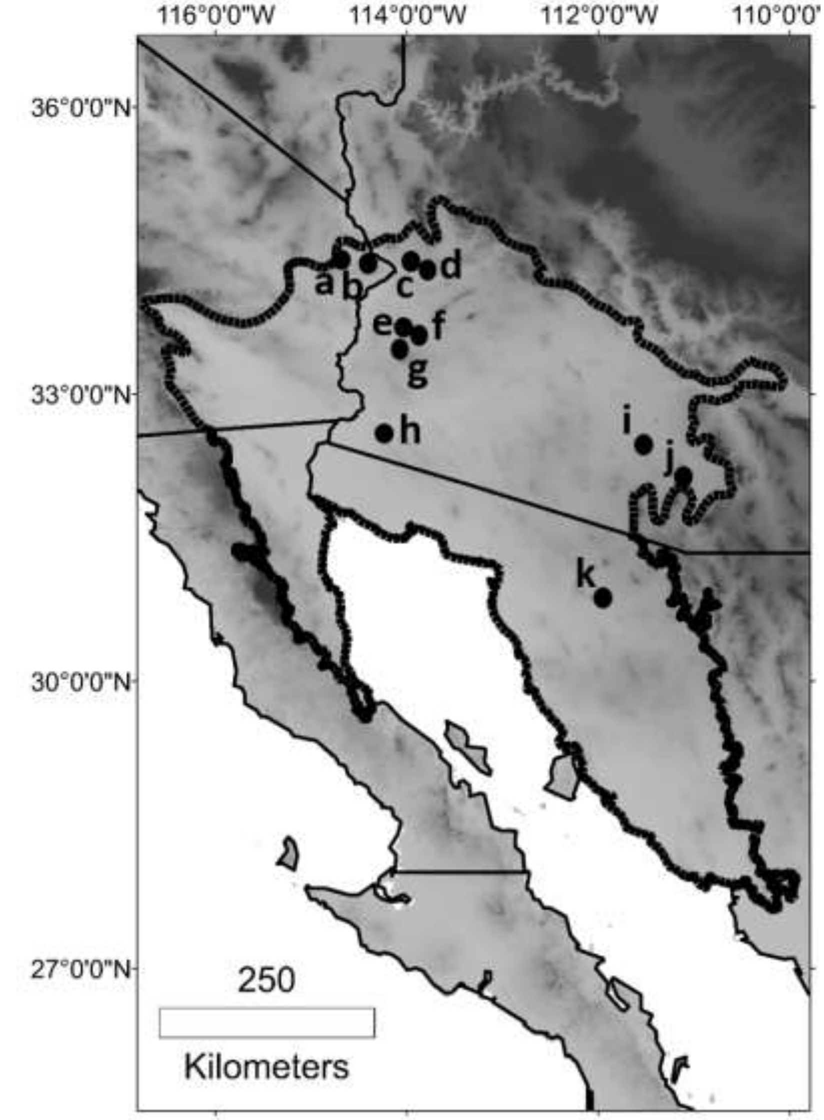


Figure 1. Localization of the sites with fossil amphibians and reptiles in the Sonoran Desert used in this study. Whipple Mountains (a), Redtail Peaks (b), Artillery Mountains (c, d), New Water Mountains (e, f), Burro Canyon and Brass Cap Point (g), Wellton Hills (h), Wolcott Peak (i), Tucson Montains (j), and Rancho la Brisca (k). Low elevation in light gray and high elevation in dark gray.

Table 1. Sites (Figure 1) and calibrates radiocarbon ages with CalPal (Danzeglocke *et al.,* 2015). *Ages calibrated by Van Devender *et al.* (1985).

Site	Ca^{14}	+/-	CalPal	+/-	min	max
Artillery Mountains	10250	200	11990	408	11582	12398
Tucson Montains	12430	400	14751	685	14066	15436
Wolcott Peak	5020	80	5775	96	5679	5871
Wolcott Peak	12130	500	14419	757	13662	15176
Wolcott Peak	14550	800	17560	952	16608	18512
Brass Cap Point	11450	400	13422	439	12983	13861
Burro Canyon	13400	250	16281	510	15771	16791
Burro Canyon	14400	330	17628	418	17210	18046
New Water Mountains	7870	750	8890	838	8052	9728
New Water Mountains	10880	900	12624	1214	11410	13838
New Water Mountains	11000	510	12778	640	12138	13418
New Water Mountains	11060	390	12935	431	12504	13366
New Water Mountains	12090	570	14411	838	13573	15249
Wellton Hills	6600	370	7436	375	7061	7811
Wellton Hills	7950	370	8873	420	8453	9293
Wellton Hills	8150	260	9051	327	8724	9378
Wellton Hills	8750	320	9841	371	9470	10212
Wellton Hills	10580	550	12212	726	11486	12938
Wellton Hills	10750	400	12486	534	11952	13020
Redtail Peaks	8910	360	10048	447	9601	10495
Redtail Peaks	9160	170	10343	219	10124	10562
Redtail Peaks	10030	160	11642	292	11349	11934
Redtail Peaks	10930	170	12897	147	12749	13044
Redtail Peaks	13810	270	16863	500	16363	17363
Rancho la Brisca	6080	250	6942	281	6661	7223
Rancho la Brisca*	nd	nd	75000	nd	75000	nd
Rancho la Brisca*	nd	nd	125000	nd	125000	nd

Amphibian and reptile communities

The list of extant amphibians and reptiles species found today in the Sonoran Desert was obtained from Phillips and Wentworth (2000), Molina-Freaner and Van Devender (2010) and Rorabaugh (2008). Fossil amphibian and reptile data were obtained from Van Devender *et al.* (1985), Van Devender and Mead (1978), and White *et al.* (2010). Names of species were updated using Frost (2015) for amphibians, and Uetz and Hallermann (2016) for reptiles. ^{14}C ages derived from studies with fossil amphibian and reptiles (Table 1), were calibrated using CalPal (Danzeglocke *et al.,* 2015). The calibrated ages were grouped in eight age classes: Recent (0 ka), mid-Holocene (5-8 ka), early Holocene (8-10 ka), Pleistocene-Holocene transition (10-12 ka), Younger Dryas (YD, 12-14 ka), Allerød/Bølling (AB, 14-17), Last Glacial Maximum (LGM, 17-23 ka) and early Wisconsinian (75-125 ka).

Paleoclimate reconstruction

We select the Mutual Climatic Range method to model the recent distribution of each fossil taxon with extant counterparts data found in the site by overlapping their distributions. We assumed that the overlapping distribution areas contained the climatic values that were present in the past, and that the climatic conditions from where the fossil community was found are represented by the overlapping of the distributions (Blain *et al.*, 2009).

We created a Species Distribution Model (SDM) using historic records of extant taxa collected and cleaned from *Sistema Nacional de Información sobre la Biodiversidad* (CONABIO; www.conabio.org.mx), Global Biodiversity Information Facility (GBIF; www.gbif.org) and matched wiht the literature (*e.g.* Taylor, 1938; Bogert and Oliver, 1945; Smith and Hensley, 1958; Conant and Berry, 1978; Grismer, 2002; Brennan and Holycross, 2006; Rorabaugh, 2008; Lemos-Espinal and Smith, 2009; Enderson *et al.*, 2009, 2010).

We builted the SDMs using MaxEnt v3.3 (Phillips *et al.,* 2006). MaxEnt provides the use of SDM to explore and predict the taxa distribution, even with a small number of records (Wisz, *et al.,* 2008). We generated ten models for each species, using *bootstrap* sampling, each model was validated with the 30% of the original records. To evaluate the models we use the Area Under de Curve (AUC) generated by the Receiver Operating Characteristic technique (ROC). We obtained the potential distribution reclassifying the potential area with 10 percentil training presence. The result was a binary map indicating the optimal climatic conditions (1= optimal, 0= not optimal) for each fossil amphibian and reptile species found in each time interval in the paleontological record of the Sonoran Desert.

We overlapped all species potential distributions shaping the amphibian and reptile communities for each time interval in ArcGis 10.0. Then, we extracted the values of the 19 bioclimatic variables from Worldclim (Hijmans *et al*. 2005; www.worldclim.org) from overlapped area, with wich we inferred the paleoclimate for each time interval.

Paleoenvironment reconstruction

Using the amphibians and reptiles incidence (presence-absence) database generated for each age group (Supplementary Table 1), we produced a Habitat Weighting analysis (Blain *et al.*, 2008) using six different habitat types: Sonoran Desert, thornscrub, deciduous tropical forest, grasslands, mountain forest and Chihuahuan Desert. Depending on how many taxa were found in each habitat type per time interval, we divided the maximum value of 1 between the numbers of habitats occupied. The sum of the habitat weighting values for each species allowed the reconstruction of the vegetation type of the distinct time intervals during the Pleistocene and Holocene.

Evolution of the amphibian and reptile communities through time

Using incidence data of amphibians and reptiles species for each age group, we obtained a distances matrix using the Chord Distance Method, tested as a good method for identifying communities that are not analogous (Bocard, *et al.,* 2011). We used the Bray-Curtis method to detect ecological changes through time (Stewart, 2008). We compared the dissimilarity index of Recent and fossil communities and with a cluster analysis we grouped the age intervals, verifying the assignment of age groups to each cluster with an Amplitude Silhouette Analysis. We performed the association between the studied age groups with a Principal Coordinate Analysis (PCoA). For the analysis we used R (R Development Core Team, 2013) with the cluster packages (Maechler, 2013) labsdy version 1.5-0 (Roberts, 2013) and vegan version 2.0-7 (Oksanen *et al.,* 2013).

Results

We obtained a database of 14 anurans, 18 lizards, 25 snakes and 6 turtles for the interval Pleistocene to Holocene in the Sonoran Desert (Supplementary Table 1). The anurans *Craugastor augusti* and *Leptodactylus melanonotus*, the lizards *Cophosaurus texanus, Holbrookia elegans, Phrynosoma modestum* and *Sceloporus undulatus,* the snakes *Coluber mentovarius, Pituophis melanoleucus* and *Sonora semiannulata,* and the turtles *Terrapene* sp. and *Kinosternon flavescens* are not found today in the Sonoran Desert, but they were in the past.

Sonoran Desert paleoenvironment through the Pleistocene-Holocene

Habitat weighting values (Table 2; Fig. 2) shows that the Sonoran Desert is today dominated by Sonoran Desert habitat and that the remaining vegetation types are structured in stripes. During the mid-Holocene a similar pattern was found but by the early Holocene. The dominance of the Sonoran Desert habitat was slightly higher than the rest of the vegetation types, showing a mosaic vegetation structure. For the early Wisconsinian the habitat weighting values increased for all vegetation types, suggesting that the vegetation structure in stripes was present in this time interval (Fig. 2).

Table 2. Habitat weighting of the amphibians and reptiles communities regarding to the habitat type that they belong in each age interval. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

Interval of time	**Sonoran Desert**	**Thornscrub**	**Tropical deciduous forest**	**Pastureland**	**Mountain forest**	**Chihuahuan Desert**
Recent	17.56	11.56	7.15	6.91	2.36	5.08
5-8 ka	10.67	7.17	4.34	6.18	4.56	3.93
8-10 ka	6.43	1.93	1.43	1.35	0	0.85
10-12 ka	6.16	4.16	1.83	2.91	1.48	1.33
12-14 ka	4.23	1.73	1.23	1.65	0.5	0.65
13-17 ka	5.29	2.79	2.29	2.96	1.16	1.46
17-23 ka	3.91	2.91	1.41	1.41	0.16	1.16
75-125 ka	5.21	6.37	5.29	3.3	1.77	2.64

Sonoran Desert paleoclimate through the Pleistocene-Holocene

Our paleoclimate reconstruction shows an important climatic variability in the Sonoran Desert throughout the Pleistocene and Holocene. The climate for the Sonoran Desert today, estimated with the Mutual Climatic Range method with amphibians and reptiles, has an annual mean temperature of 22.25°C and an annual precipitation of 167.48 mm/year (Table 3, Fig. 3). The maximum temperature is 40.39°C in July and the minimum is 5.38°C in December. The largest amount of precipitation is 81.80 mm between the months of July to September and the drier months have a precipitation of 8.33 mm in April-June. The values reconstructed with the Mutual Climatic Interval method for today agreed with the climatic data for the Sonoran Desert of the Western Regional Climate Center (www.wrcc.dri.edu), Rzedowski (2006) and Brito Castillo *et al.* (2010).

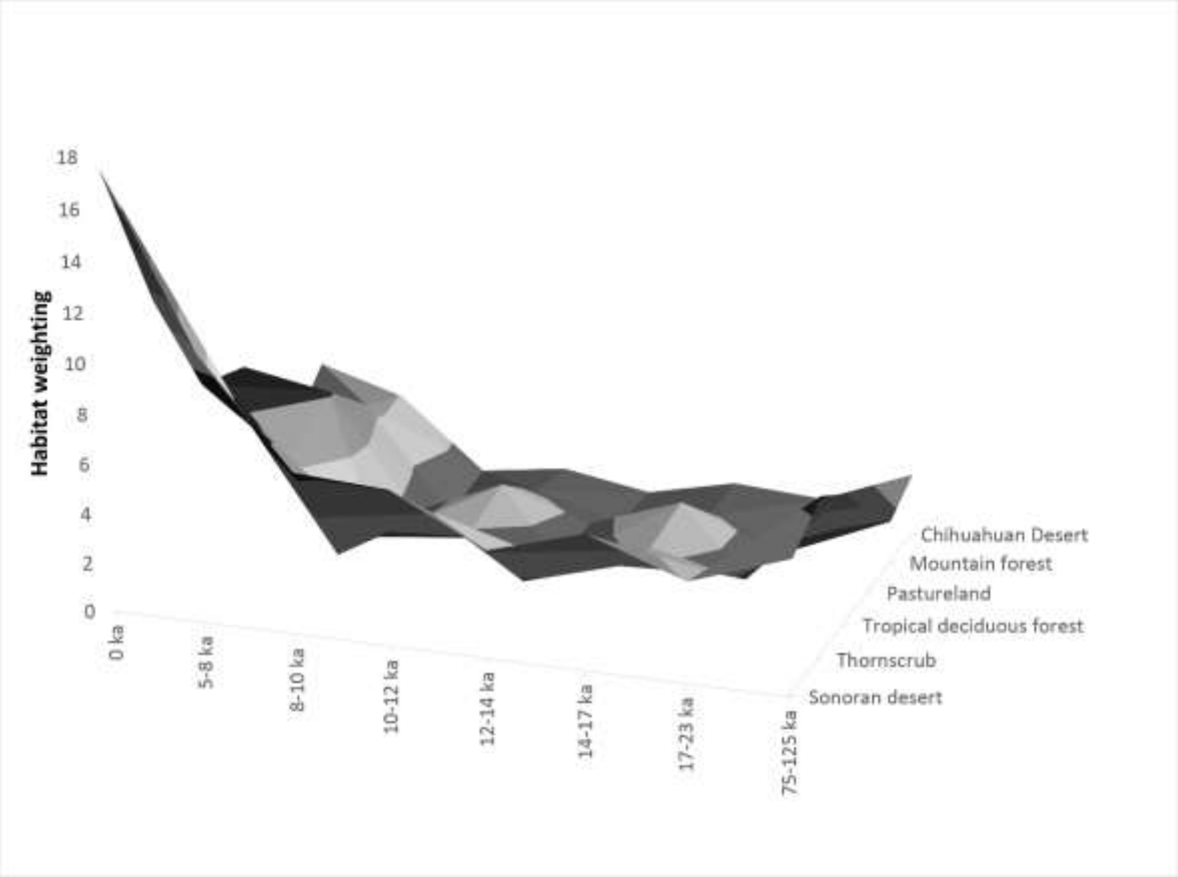


Figure 2. Change in the vegetation structure in the Sonoran Desert during the Pleistoene and Holocene as revealed the Habitat Weighting analysis using amphibian and reptiles data as proxies. A stripe vegetation structure is predicted for the early Wisconsinian. During the Pleistocene to early Holocene increasing the heterogeneity of habitats to mosaic structure. A stripe vegetation is observed again from the mid-Holoceno to the Recent. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

The annual mean temperature values calculated for all studied age intervals turned out to be always below to those of today (Fig. 3, Table 3). For the mid-Holocene the temperature was 2.75°C lower and for the early Holocene and the Pleistocene-Holocene transition 1°C lower, but for YD the temperature decreased up to 5.71°C less, and for the early Wisconsinian 6.71°C. During the Allerød/Bølling and the LGM the temperature was just 2°C lower (Fig. 3, Table 3).

In the early Wisconsinian, YD and, mid-Holocene, the annual precipitation increased associated to temperature drop. But in early Holocene, Pleistocene-Holocene, Allerød/Bølling and LGM, the precipitation was lower compared with that of today, showing drier climates (Fig. 3, Table 3).

Temperature variables are lower in the YD and in the early Wisconsinian, except for the temperature for July-September that in the early Wisconsinian was 5.99°C higher than today (Fig. 4). The precipitation variables increased in those age intervals with higher temperature decrements (mid-Holocene, YD and early Wisconsinian), except for the precipitation during the coldest months (December-February) in the early Wisconsinian, with the lowest estimated precipitation of 17.86 mm (Fig. 5).

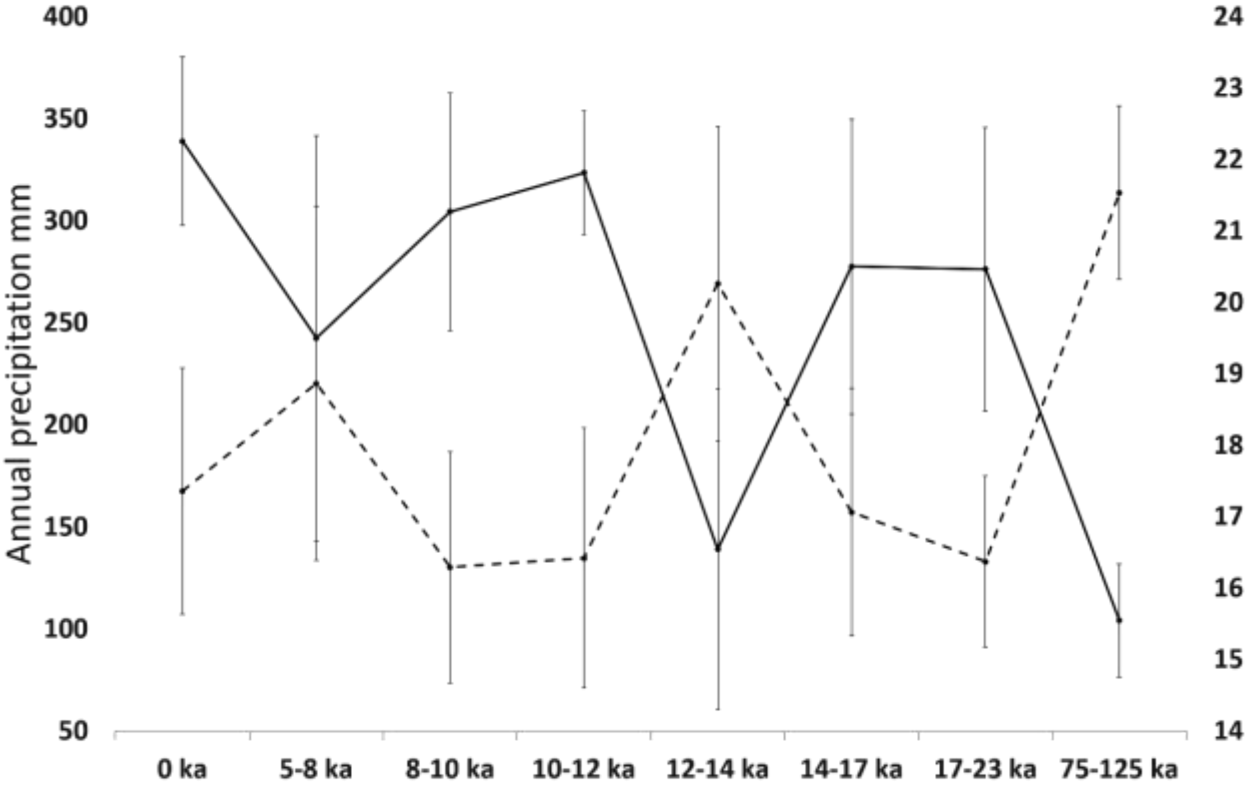
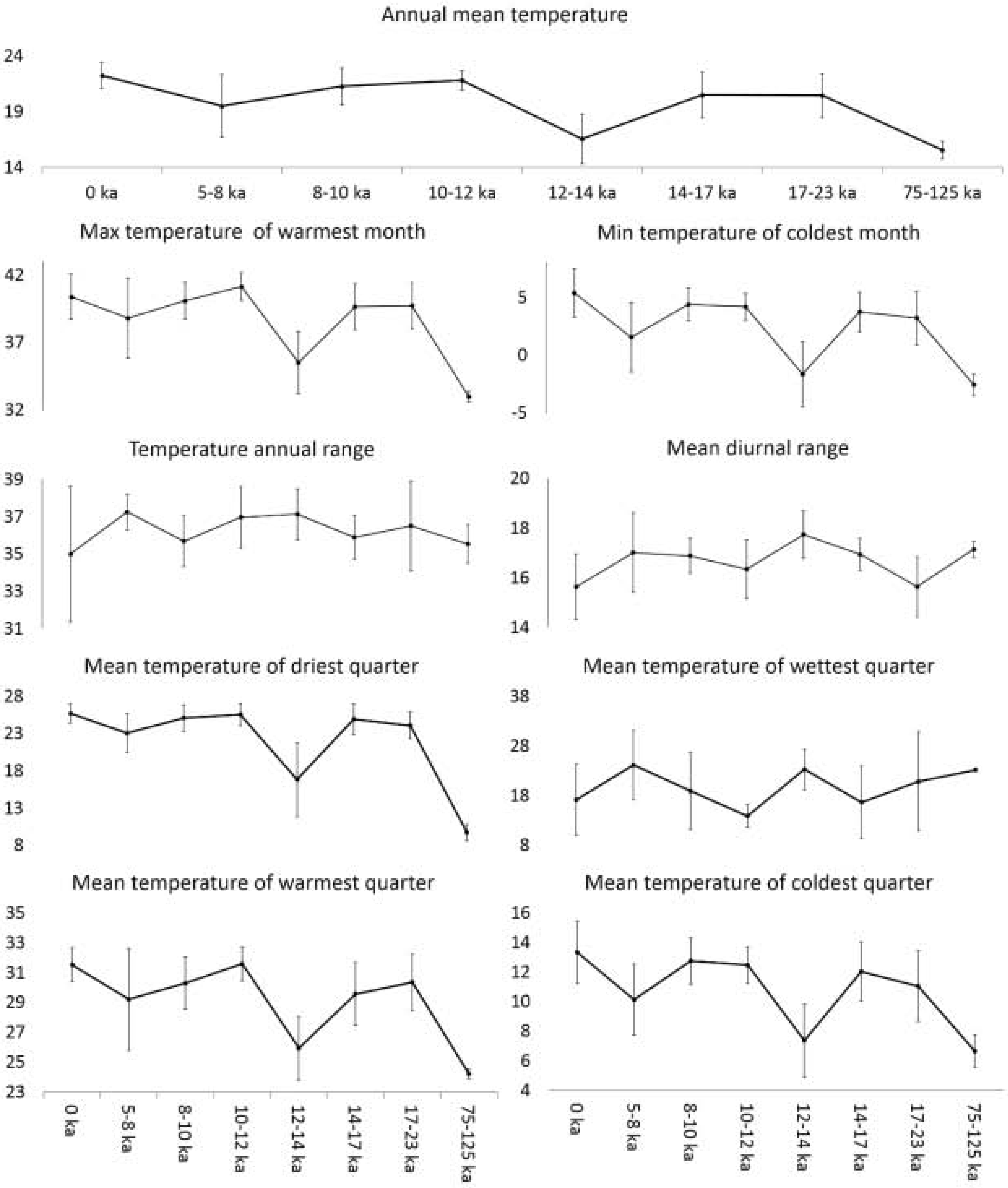


Figure 3. Annual mean temperature reconstruction (solid line) and annual precipitation (dotted line), by means of amphibians and reptiles, through the Pleistocene and Holocene of the Sonoran Desert. The error bars show the standard deviation. 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

Table 3. Temperature (°C) and precipitation (mm) climate values inferred for the Sonoran Desert through the Pleistocene and Holocene. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

Intervale of time	**0 ka**	**5-8 ka**	**8-10 ka**	**10-12 ka**	**12-14 ka**	**14-17 ka**	**17-23 ka**	**75-125 ka**
Annual mean temperature	22.25	19.50	21.27	21.81	16.54	20.50	20.46	15.54
Mean diurnal range	15.64	17.01	16.88	16.34	17.74	16.94	15.64	17.14
Max temperature of warmest month (July)	40.39	38.80	40.10	41.16	35.49	39.64	39.72	32.97
Min temperature of coldest month (December)	5.387	1.54	4.41	4.19	-1.64	3.74	3.21	-2.57
Temperature annual range	35.00	37.26	35.69	36.97	37.13	35.90	36.51	35.54
Mean temperature of wettest quarter (July-September)	17.16	24.16	18.90	13.88	23.26	16.65	20.83	23.15
Mean temperature of driest quarter (April-June)	25.69	23.05	25.09	25.55	16.83	24.91	24.06	9.70
Mean temperature of warmest quarter (June-August)	31.52	29.21	30.29	31.59	25.93	29.56	30.35	24.20
Mean temperature of coldest quarter (December-February)	13.34	10.12	12.75	12.47	7.37	12.04	11.06	6.66
Annual precipitation	167.48	220.21	130.13	134.64	269.16	157.08	132.85	313.70
Precipitation of wettest month (August)	34.04	43.62	22.15	20.98	53.12	26.44	22.42	59.31
Precipitation of driest month (May)	1.01	2.68	0.28	0.97	4.54	0.50	1.30	6.64
Precipitation of wettest quarter (July-September)	81.80	104.25	58.24	53.62	137.40	71.01	54.11	164.57
Precipitation of driest quarter (April-June)	8.33	14.60	6.23	8.00	20.05	8.41	8.90	25.59
Precipitation of warmest quarter (July-August)	60.26	83.37	27.47	29.57	111.58	29.02	36.45	148.20
Precipitation of coldest quarter (December-February)	51.82	55.60	53.72	50.87	54.07	65.86	45.01	33.96


Annual mean temperature

Max temperature of warmest month

Min temperature of coldest month

Temperature annual range

Mean diurnal range

Mean temperature of driest quarter

Mean temperature of wettest quarter

Mean temperature of warmest quarter

Mean temperature of coldest quarter

Figure 4. Pleistocene and Holocene temperature variables reconstructed from the mutual climatic range method with amphibian and reptiles of the Sonoran Desert. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

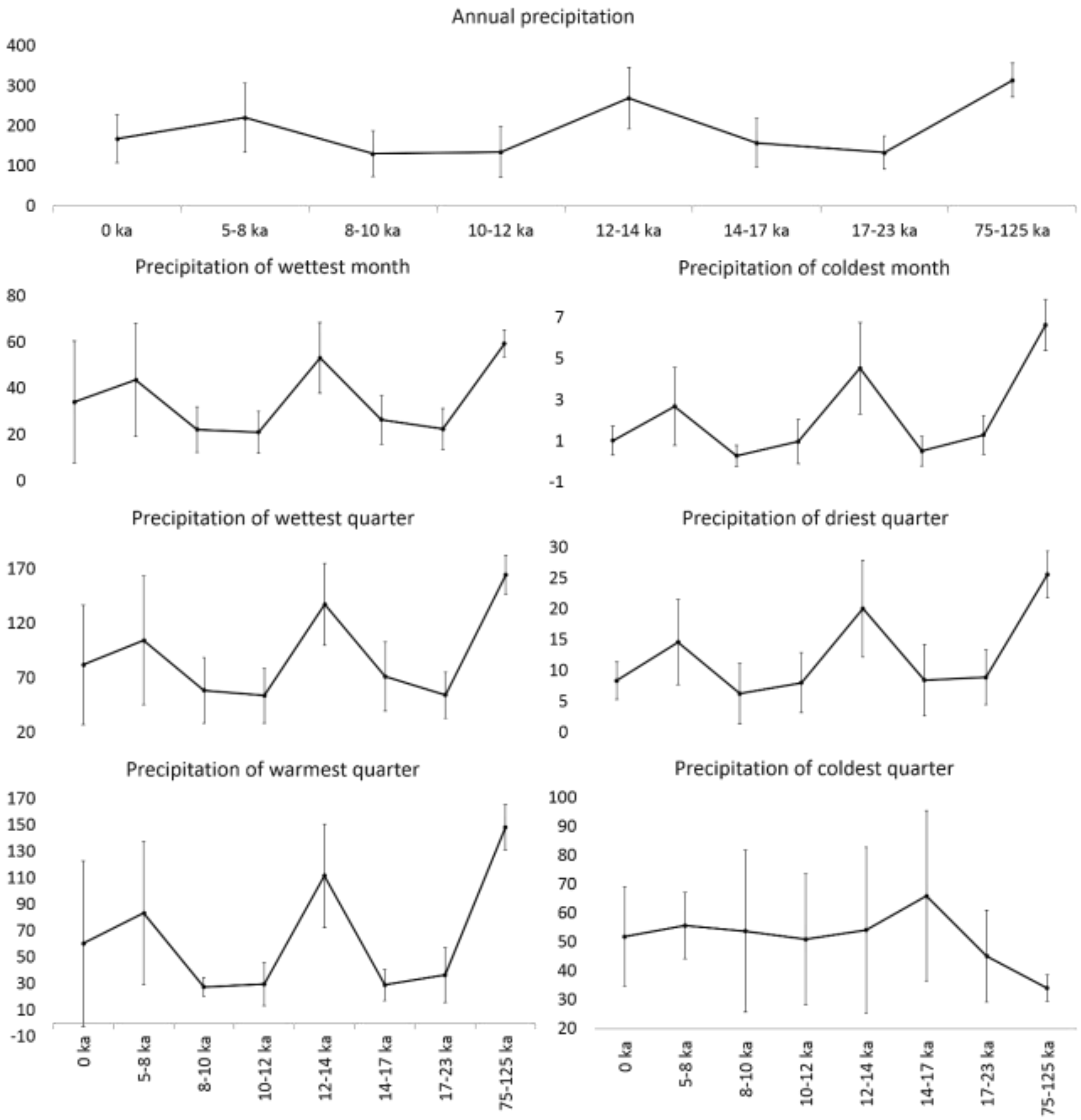


Figure 5. Pleistocene and Holocene precipitation variables reconstructed from the mutual climatic range method with amphibian and reptiles of the Sonoran Desert. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

Evolution of the amphibian and reptile communities in the Sonoran Desert through the Pleistocene-Holocene

Distance between age intervals with Chord Distance and Bray-Curtis analyses were similar using both methods. Dissimilarity values obtained by the Chord Distance and Bray-Curtis methods showed the ecological distance between the composition of the amphibian and reptiles communities today and the studied age intervals (Table 4, Fig. 6). Hereinafter Chord Distance values will be used for analysis of the results.

Table 4. Dissimilarity matrix between the different age groups during the Holocene and Pleistocene. Values the matrix above the diagonal are Bray Curtis index and the values below the diagonal are cord distance index. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

	0 ka	**5-8 ka**	**8-10 ka**	**10-12 ka**	**12-14 ka**	**14-17 ka**	**17-23 ka**	**75-123 ka**
0 ka	0	0.309	0.564	0.482	0.652	0.554	0.544	0.451
5-8 ka	0.319	0	0.625	0.579	0.538	0.473	0.560	0.740
8-10 ka	0.662	0.680	0	0.796	0.361	0.423	0.565	0.884
10-12 ka	0.549	0.607	0.364	0	0.851	0.529	0.574	0.764
12-14 ka	0.746	0.625	0.429	0.857	0	0.288	0.619	0.937
14-17 ka	0.623	0.518	0.565	0.529	0.308	0	0.623	0.850
17-23 ka	0.656	0.633	0.892	0.586	0.619	0.630	0	0.819
75-123 ka	0.487	0.746	0.364	0.767	0.943	0.854	0.833	0

The Early Wisconsinian dissimilarity values among composition of amphibian and reptiles communities with regard to the Recent were lesser than the Pleistocene. This age interval showed the most drastic climate changes. The annual mean temperature was 6.71°C lower and the precipitation was 146.22 mm higher than today; and the vegetation structure tend to stripes type, as is today.

In the YD we found the greatest dissimilarity values of amphibian and reptiles communities with respect to the Recent. In this age period, the mosaic vegetation structure was present but there were drastic changes in the climate. The annual mean temperature was 5.71°C lower, but the annual precipitation was 101.68 mm higher than today. The dissimilarity values between amphibians and reptiles compositions were close between the Allerød/Bølling and LGM, and the mosaic vegetation structure is present. However, the annual mean temperature was 1.75°C and 1.79°C lower, and the precipitation 10.4 mm and 34.63 mm lower than today, respectively.

today (Fig. 2, 6 C).

The early Holocene to LGM presents dissimilarity values of amphibian and reptiles communities above to 49% of dissimilarity with respect to the Recent. These age intervals have associated the vegetation structure towards a mosaic, although climatic values did no differ much from today. Then, in the early Holocene the annual mean temperature and the annual precipitation were just 0.98°C and 37.35 mm lower with respect to the Recent, respectively. In the Pleistocene-Holocene transition the dissimilarity values among amphibians and reptiles communities decreased with respect to early Holocene. Climate in the Pleistocene-Holocene transition showed 0.44°C decrement in the annual mean temperature and a 32.84 mm in the annual precipitation than today, however a mosaic vegetation structure remains (Fig. 2, 6).

The mid-Holocene showed the lowest dissimilarity values with respect to the Recent, indicating few changes in the amphibians and reptiles community structure. During the mid-Holocene the mean annual temperature was 2.76°C below and annual precipitation 52.75 mm above the Recent climate (Fig. 6 A, B). In spite of climatic differences between both age intervals, it appears to be that climate modifications through time have not affected the composition of the amphibians and reptiles communities in a great scale, possibly because the vegetation was structured in stripes during the mid-Holocene as it is found

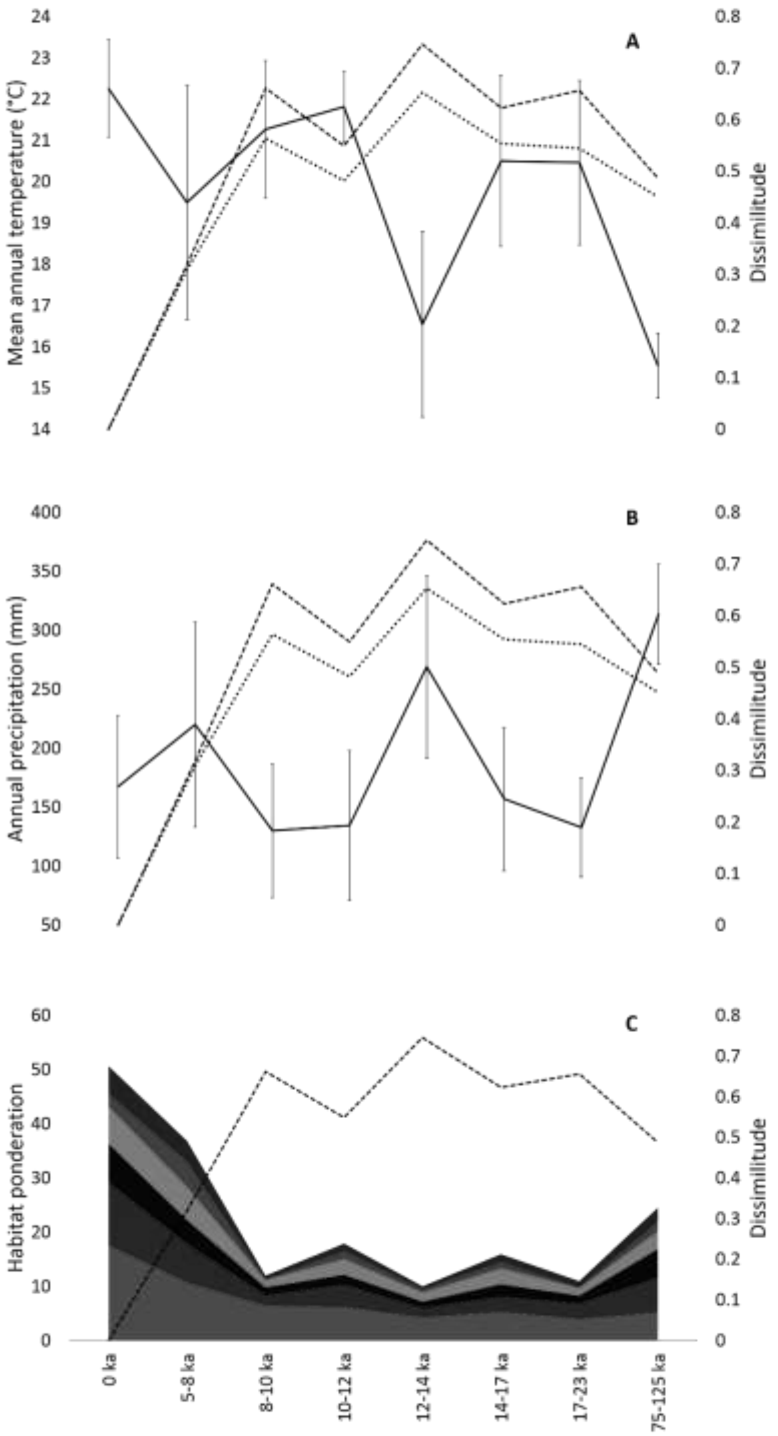


Figure 6. Chnages in annual temperature (A), annual precipitation (B), and vegetation structure (C) through time, comparing past amphibiand and reptile communities with the Recent, using Chord Distance values (segmented line) and Bray-Curtis values (dotted line). In C, gray scale shows bottom up: Sonoran Desert, thornscrub, deciduous tropical forest, grasslands, mountain forest and Chihuahuan Desert. 0 ka = Recent, 5-8 ka = mid-Holocene, 8-10 ka = early Holocene, 10-12 ka = Pleistocene-Holocene transition, 12-14 ka = Younger Dryas, 14-17 ka = Allerød/Bølling, 17-23 ka = Last Glacial Maximum, 75-125 ka = early Wisconsinian.

PCoA showed the relationship of the vegetation structure (X axis, CoA1) and the climate variables (Y axis, CoA2). According to this analysis, in quadrant I the Recent and the Early Wisconsinian was defined by a vegetation structure in stripes and strong influence of the climatic variables. In quadrant II, the mid-Holocene and the Pleistocene-Holocene transition was definided by the vegetation structure in stripes and slight climatic variables influence. In Quadrant III, the early Holocene and the Younger Dryas was defined by a vegetation structured in mosaic and strong influence of climatic variables. In quadrant IV, the Allerød/Bølling is defined by a vegetation structure in mosaic and little climatic variables influence (Fig. 7).

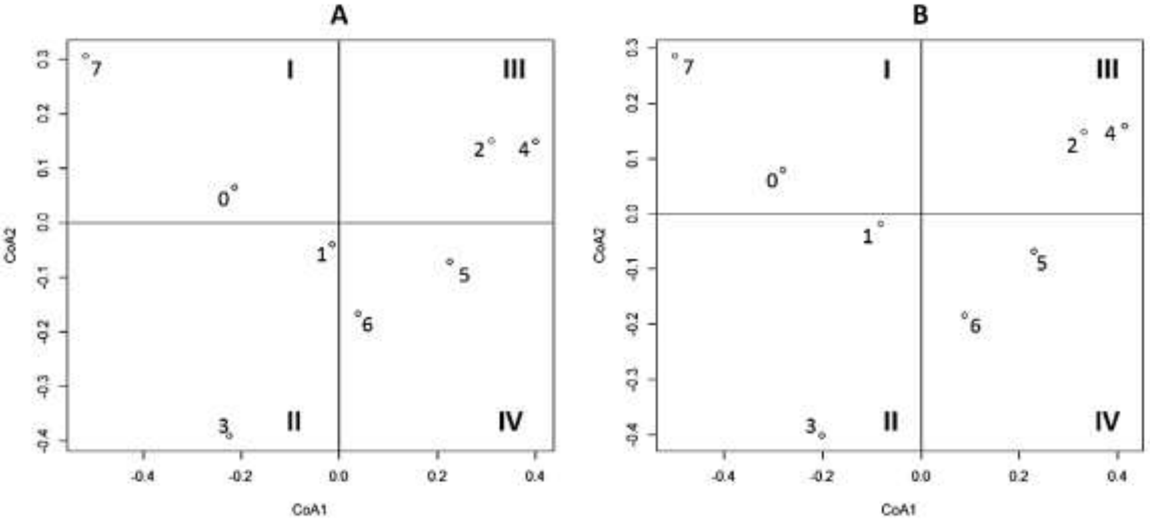


Figure 7. Principial coordinates analysis (PCoA) made with the chord distance (A) and Bray-Curtis (B) methods. The PCoA area was divided in four quadrants inferring the variables that affected amphibian and reptile communities for each age group: I. Stripe vegetation structure and strongly affected by climate, II. Stripe vegetation structure and slightly influenced by climate, III. Mosaic vegetation structure and strongly influenced by climate, IV. Mosaic vegetation structure and slightly influenced by climate. In both cases, results were similar. 0 = Recent, 1 = mid-Holocene, 2 = early Holocene, 3 = Pleistocene-Holocene transition, 4 = Younger Dryas, 5 = Allerød/Bølling, 6 = Last Glacial Maximum, 7 = early Wisconsinian.

Discussion

Paleoclimate evolution of the Sonoran Desert

The climate reconstruction for the early Wisconsinian our estimated mean annual temperature lower than today agreed with data of the Greenland ice sheet (Dahl-Jensen *et al.*, 1998). Our annual precipitation estimated with a more humid climate than today, agreed with that for Babícora (around

79-85 ka; Roy *et al.*, 2013), being the only paleopreciptation datum available for the region in this age interval.

For the Allerød/Bølling and the LGM, we inferred that the average mean temperature was about 2°C lower, and annual precipitation was also lower compared to the Recent (Table 3, Fig.3). A lower temperature is consistent with the suggested of Kirby *et al.* (2013), that during the Allerød/Bølling the precipitation was realtively higher during the winter (Table 3, Fig. 4), and even lower during the LGM (Roy *et al.,* 2014). For both age intervals we predicted a lower summer precipitation than today (Table 3, Fig. 4) agreeing with Roy *et al.* (2012, 2013), but not Kirby *et al.* (2013) results, who suggested a higher precipitation.

For Younger Dryas we predicted that the annual mean temperature was 5.71°C lower, and the annual precipitation greater compared to the Recent (Table 3; Fig. 3). Our data agree with the "great cooling" suggested by Kirby *et al.* (2013), during this time interval in which temperatures was 5-6°C less compared to the Recent (Metcalfe, 2006; Fiedel, 2011). We inferred that precipitation was considerably higher during the summer (Table 3, Fig. 4), affecting positively the annual precipitation in the Sonoran Desert (Roy *et al.,* 2013). Concurring with Metcalfe (2006) and Antiano and McDonald (2013), there are no changes in the winter precipitation, as our results show. During the Younger Dryas the climate during this age interval was similar to "El Niño" with an important influence of the Gulf of California (Antiano and McDonald, 2013).

In the Pleistocene-Holocene transition we inferred that the mean annual temperature was similar to the Recent, but the annual precipitation was lower (Table 3, Fig. 3). Our data agreed with a dry and hot weather, as inferred with speleothems in Arizona (Antiano and McDonald, 2013) and with diatoms in Guaymas (Roy *et al.*, 2014). Both, Roy *et al.* (2012, 2013, 2014) and Antiano and McDonald (2013) showed evidence that during the Pleistocene-Holocene transition there was a higher precipitation, contrary to our findings.

In the early Holocene we predicted that temperature was almost 1°C lower and that the precipitation decrease was also lower, compared to the Recent. There is a controversy It has been suggested that in the early Holocene, there were either humid (Anderson and VanDevender, 1995; Roy *et al.* 2012;

Antiano and McDonald, 2013) or arid (Antiano y Mcdonald, 2013) conditions, and that the variability of “El Niño” was similar to the one today (Antiano and McDonald, 2013). However, both hypothesis agreed with our data in that the surface ocean temperature was lower than today (Barron, *et al.,* 2012). Using fossil pollen evidence McAuliffe and VanDevender (1998) and Metcalfe (2006), results contrast with these evidence suggesting that for this age interval the temperature was 2°C higher than today.

For the mid-Holocene, the climatic recostrunction suggested a mean annual temperature 2.75°C lower and, annual and summer precipitations higher than today (Table 3, Fig. 3, 4). Contrary to our results McAuliffe and Van Devender (1998), Metcalfe (2006) and Barron *et al.* (2012), predicted that the temperature in the Sonoran Desert was 2 °C higher than today by using paleovegetation as a proxy. However their estimation does not matches with Antiano and McDonald (2013) finding in which is known that during the mid-Holocene the temperature of the ocean surface decreased. Our results also agreed with a more humid climate for the mid-Holocene (Anderson and Van Devender, 1995; McAuliffe and Van Devender, 1998; Metcalfe, 2006). The summer precipitation appears to be highly influential in the annual precipitation (Barron *et al.*, 2012; Roy *et al.*, 2012; Antiano and McDonald, 2013) as it is predicted by our data (Table 3, Fig. 4). A higher precipitation was possibly caused by the contribution of the effect of North American monsoon (Poore *et al.*, 2005; Barron *et al.*, 2012), that is believed to become very important during the mid-Holocene (Roy *et al.,* 2012), associated to the displacement of the intertropical convergence zone (ZITC) to the north (Barron *et al.*, 2012) with a higher influence of the Gulf of Mexico than that of the Gulf of California in the past (Antiano and McDonald, 2013).

Vegetation structure for the Pleistocene-Holocene in the Sonoran Desert

Clark *et al*. (2012) indicated that for North America the change of the vegetation structure occurred in the 16-11 ka interval. In contrast, we predicted that a mosaic vegetation structure with grasslands and open forests persisted from the LGM up to the early Holocene and that the change from a mosaic vegetation structure to a stripe vegetation structure occurred during the mid-Holocene, remaining until today (Fig. 2, 6 C).

Our data agreed with other published information: Williams *et al.* (2004) using fossil pollen data inferred that the LGM in southeastern North America was dominated by open forests and grasslands; Anderson and van Devender (1998) indicated that the vegetation structure that exists today was established between the 9300-5400 BP;, and Hall *et al.* (1988) suggested that pine and junipers forests existed in the Sonoran Desert in the 15-16 ka interval, and were mixed with the Sonoran Desert vegetation during the 11-8 Ka and in the 10-5 ka a more humid Sonoran Desert was established (Fig. 2, 6 C). We believe that the Sonoran Desert as structured today was established in the last 4 ka (Hall *et al.*, 1988; McAulifle and VanDevender, 1998, Metcalfe, 2006).

Guthrie (1984) proposed that the megafauna was an important factor in the construction of the mosaic vegetation, combining open forests and a greater plant diversity compared to that found today. Large mammals have effected on vegetation coverage, seed dispersal, nutrient cycles and fire regimens; also, because of their dispersal capacity, megafauna may have increased the environmental heterogeneity (Johnson, 2009a; Faith, 2011; Gill, 2014).

Studies with fungus spores *Sporormiella* indicated a synchronic event in which an important change in the vegetation structure was associated to a large carbon accumulation caused by a larger number of fires following the extinction of the megafauna (Gill *et al.*, 2009, 2012; Gill, 2014). Today, fires are considered as the primary abiotic force affecting vegetation structure (Gill, 2014). When the megafauna was present, fires were fewer because megaherbivores diminished the accumulation of ignitable leaf litter and vegetal material (Faith, 2011; Gill, 2014). However, it is believed that during the early and mid-Holocene, the extinction of the megafauna together with the influence of the first humans inhabitanting the Americas may have influenced on the fire regimens in a local way only (Marlon *et al.*, 2013). Anthropogenic activity, together with climate factors was more influencial during the Late Holocene (3000 BP) (Power *et al.*, 2008; Pausas and Keeley, 2009; Marlon *et al.*, 2009, 2013; Pinter *et al.*, 2011).

It can be predicted that the change in the vegetation structure must have occurred during the North American megafauna extinction dated between ~13800-11400 BP cal (12000-10000 BP ^{14}C) (Faith and Surovell, 2009; Haynes, 2013; Johnson, 2013; Faith, 2014). However our data suggest that in the Sonoran Desert the vegetation structure changed during the early Holocene (8-10 ka). These data disagree with our findings where the vegetation structure change during the early Holocene (8-10 ka). Then, we think that the change of vegetation from a mosaic structure to a stripes structure was rather produced by the climate change. Another possibility is that the extinction of the megafauna in the Sonoran Desert, scarcely studied in this region (Barnosky *et al.*, 2014), may have occurred later than as generally proposed for North America.

Ecological change of amphibian and reptilian communities in the Sonoran Desert through the Pleistocene-Holocene

The only study to understand the transition of small vertebrates in the Pleistocene-Holocene transition was by Blois *et al.* (2010) who found local extinction, loss and gain of species, and changes in the abundance of small mammal communities through time. They predicted that changes in the community structure were consequences of megafaunal extinction and climate change, together. However our results show that vegetation structure is the main factor that modified the structure of amphibian and reptilian communities, followed by climate change. Certainly, the tight interactions between the vegetation structure and the amphibian and reptiles community composition lessened the climate change effects.

In the Sonoran Desert, the amphibian and reptilian communities were affected in first place by the vegetation structure and then by the climate. The greater dissimilarities of the amphibian and reptiles communities with the Recent (>0.49) occurred during the mid-Holocene when the vegetation structure changed from a mosaic type to the stripes type found today. Small vertebrates cannot alter the environment in a significant way, but changes in vegetation structure caused by any mean (e.g. extinction of megafauna or climate) can affect the communities of small vertebrates since their biology are tightly linked to these factors (Gill, 2014).

Plants do not only provide food to herbivores, but they also provide habitat to other biological components in the ecosystem (Willis and McDonald, 2011). They modify the habitat creating microhabitats that would lessen the effects of climate change by enhancing favorable microclimates ofr many species (Pontes *et al.*, 2013; Scheffers *et al.*, 2014). Bromelias are generally used by amphibians for breeding or resting sites; phytotelms allow to lessen the air temperature from 93 to 100% of each 1°C air temperature increases, enhancing conditions for the adult amphibians and providing the necessary humidity in dry weather (da Silva *et al*. 2011; Pontes *et al.*, 2013); and *Agave spp.* provide resting place to anurans such as *Plectrohyla ameibothalame* (Canseco-Marquez *et al.*, 2002).

Lizard species can maintain their preferred body temperatures through behavioral thermoregulation and habitat selection (Grigg y Buckley, 2013). Some Chihuahuan and Sonoran desert species of *Phrynosoma* and other phrynosomatid lizards display crepuscular activity as a adaptive mechanism for escaping the effects of climate warming (Lara-Resendiz *et al*. 2013, 2015). *Sceloporus undulatus speari* used a thermoregulation behavior by perching in a sun/shadow mosaic within the vegetation to mitigate the heat, whereas in cooler seasons it uses perches with direct solar incidence (Lemos-Espinal *et al.*, 2003). The interaction of the vegetation structure and lizard species may affect the abundance of each species within the community. Open areas where the temperature is higher benefits *Anolis carolinensis*, fallen trunks benefits *A. carolinensis* and *Sceloporus undulatus*, the decrement of leaf litter in the ground favors *S. undulatus* and none of the conditions mentioned above favors *Scincella lateralis* which prefers a larger canopy coverage and the presence of leaf litter on the ground (Sutton *et al.*, 2014).

It is clear that amphibians and reptiles have tight biotic interactions with the vegetation structure where they live in. These interactions reduced the effect of communities against climate change, reducing the effect of increments and reduction of temperature and precipitation. These changes have happened in the past and surely will occur in the future.

Conclusions

During the Holocene, the Sonoran Desert was drier and warmer than in the Pleistocene, except for the mid-Holocene where the temperature decrease and the precipitation increased. Changes in vegetation structure does not seem to be directly associated to the megafauna extinction interval for North America, even though the Sonoran Desert region has been poorly studied.

Through time, amphibian and reptile communities respond first to changes in the vegetation structure and then to climate changes. Biotic interactions between vegetation and amphibians and reptiles could have had an important role to lessen the climate change effects in the past.

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Supplementary Table 1. Fossil and Current amphibians and reptiles founded in the Quaternary of the Sonoran Desert.

Taxa	**Recent**	**5-8 ka**	**8-10 ka**	**10-12 ka**	**12-14 ka**	**14-17 ka**	**17-23 ka**	**75-125 ka**
Anaxyrus cognatus	1	0	0	0	0	0	0	1
A. kelloggi	1	0	0	0	0	0	0	1
A. punctatus	1	1	0	1	0	1	0	0
A. woodhousii	1	1	0	0	0	0	0	0
Incilius alvarius	1	0	0	0	0	0	0	1
I. mazatlanensis	1	0	0	0	0	0	0	1
Craugastor augusti	0	0	0	0	0	0	0	1
Hyla arenicolor	1	0	0	0	0	0	0	1
Smilisca fodiens	1	0	0	0	0	0	0	1
Leptodactylus melanonotus	0	0	0	0	0	0	0	1
Gastrophryne olivacea	1	0	0	0	0	0	0	1
Lithobates sp.	1	1	0	0	0	0	0	1
Scaphiopus couchii	1	1	0	0	0	0	0	1
Spea hammondii	1	1	0	0	0	0	0	0
Crotaphytus collaris	1	1	0	1	0	1	0	0
Gambelia wislizeni	1	0	0	1	0	0	0	0
Coleonyx variegatus	1	1	1	1	0	0	0	0
Heloderma suspectum	1	1	0	0	0	0	0	0
Dipsosaurus dorsalis	1	1	1	0	1	0	1	0
Sauromalus ater	1	1	0	0	0	0	0	1
Callisaurus draconoides	1	1	0	0	0	0	0	0
Cophosaurus texanus	0	1	0	0	0	0	0	0
Holbrookia elegans	0	1	0	0	0	0	0	0
Phrynosoma modestum	0	1	0	0	0	0	0	0
Phrynosoma solare	1	1	0	0	0	0	0	0
Sceloporus clarkii	1	1	0	0	0	0	0	1
Sceloporus magister	1	1	0	1	1	1	1	0
Sceloporus undulatus	0	1	0	1	1	1	0	0
Urosaurus graciosus	1	0	1	0	0	0	0	0
Urosaurus ornatus	1	1	0	0	0	0	0	0
Uta stansburiana	1	0	0	1	0	0	0	0
Aspidoscelis sp.	1	1	0	1	0	0	1	0
Aspidoscelis tigris	1	1	0	1	0	0	1	0
Boa constrictor	1	0	0	0	0	0	0	0

Lichanura trivirgata	1	0	0	1	0	0	0	0
Arizona elegans	1	1	1	0	1	1	0	0
Chionactis occipitalis	1	1	1	0	1	1	0	0
Coluber flagellum	1	0	0	0	0	0	0	0
Coluber mentovarius	0	0	0	0	0	0	0	1
Coluber sp.	1	1	0	1	0	0	1	1
Gyalopion canum	1	1	0	0	0	0	0	0
Hypsiglena torquata	1	1	1	0	1	1	1	1
Lampropeltis getula	1	1	0	0	0	1	0	0
Lampropeltis pyromelana	0	1	0	0	0	0	0	0
Phyllorhynchus decurtatus	1	1	1	0	0	0	1	0
Phyllorhynchus sp.	1	1	1	0	1	1	0	0
Pituophis melanoleucus	0	1	0	1	0	1	0	0
Rhinocheilus lecontei	1	1	0	0	1	1	1	0
Salvadora sp.	1	0	0	1	0	0	0	1
Sonora semiannulata	0	0	1	0	1	1	0	0
Thamnophis cyrtopsis	1	0	0	0	0	0	0	1
Thamnophis sp.	1	0	0	0	0	0	0	1
Trimorphodon biscutatus	1	1	1	0	1	1	0	0
Rena humilis	1	1	0	0	0	0	1	0
Crotalus atrox	1	1	0	1	0	0	0	1
Crotalus cerastes	1	0	0	1	0	0	0	0
Crotalus scutulatus	1	1	0	0	0	0	0	0
Crotalus sp.	1	1	0	1	0	1	0	1
Terrapene sp.	0	0	0	0	0	0	0	1
Kinosternon arizonense	1	0	0	0	0	0	0	0
Kinosternon flavescens	0	0	0	0	0	0	0	1
Kinosternon sonoriense	1	0	0	0	0	0	0	1
Gopherus agassizii	1	0	1	1	0	1	1	0
Gopherus sp.	1	0	1	1	0	1	1	1

CAPÍTULO IV

RECONSTRUCCIÓN DE CLIMAS PASADOS UTILIZANDO EL CENTROIDE DE NICHO Y PATRONES DE ABUNDANCIA

(*Palaeontologia Electronica:* En revisión)

RECONSTRUCTION OF PAST CLIMATES USING NICHE CENTROIDS AND PATTERNS OF ABUNDANCE

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ABSTRACT

To study the past, present and future of ecological systems is necessary consider the biotic components such as species, populations, communities, biotic interactions, human activities and, the abiotic components such as the climate, soil, topography, water temperature, etc. Considering these also are important to reconstruct ecological systems, paleoclimate and paleoenvironments, thus exploring the ecological theory in the past. Ecological features are very susceptible to environmental modifications, and among these, it is expected that demography is the first to be affected during events of climate change. Paleoclimatic reconstructions with vertebrates have never used the species abundance as an ecometric to infer past climates. Theoretically, a species is expected to reach their highest abundance in the center of their climate niche, declining in abundance toward the climate niche edges. Here we use the Distance to the Niche Centroid approach (DNC), to reconstruct the climate shifts through different stratigraphic layers during the Quaternary in Loltún Cave, Yucatán by inferring abundance shifts of the Yucatan small-eared shrew *Cryptotis mayensis*. The paleoclimatic reconstruction suggests an interstadial in the XII layer where the climatic conditions were slightly colder and more humid than today. In layers X-VIII, we found the Last Glacial Maximum (LGM) with a mean annual temperature (MAT) 4.15ºC colder and an annual precipitation (AP) 1945.94 mm higher than the present one. In layers VII-VI, the MAT is 3ºC higher than in the LGM layer and the AP is variable in accordance with the Bølling-Allerød. The Younger Dryas founded in layer V has similar climatic conditions to LGM. Finally, the most recent layers (IV-I) have a similar MAT and an AP lower than to today, representing ages posterior to the Early Holocene. The use of abundance as an ecometric to reconstruct the paleoclimate is an optional tool for reconstruct past environments.

Keywords: Niche Centroid, abundance, ecometric, palaeoclimate, Yucatán Peninsula.

RESUMEN

Los estudios de sistemas ecológicos en el presente, pasado y futuro requieren la consideración de componentes bióticos como las especies, poblaciones, comunidades, interacciones bióticas, actividades humanas y, del conocimiento de los componentes abióticos como el clima, suelo, topografía, temperatura del agua y más. Lo anterior puede ayudarnos a reconstruir el paleoclima y los paleoambientes, explorando así la teoría ecológica en el pasado. Las reconstrucciones paleoclimáticas realizadas con vertebrados nunca han utilizado la abundancia de las especies, como ecométrico, para inferir climas pasados a pesar de que las características demográficas son las primeras en ser afectadas durante eventos de cambios ambientales. La abundancia de las especies es mayor en el centro de su nicho ambiental y se hace menor conforme se acerca a los extremos del mismo. En el presente estudio utilizaremos la Distancia al Centroide de Nicho (DCN) y los datos de abundancia relativa actual y fósil de la musaraña *Cryptotis mayensis* para reconstruir el clima durante el Cuaternario de la Gruta de Loltún, Yucatán. La reconstrucción paleoclimática sugiere un interestadial en la capa XII con condiciones ligeramente más frías y más húmedas que las actuales. En las capas X-VIII se encuentra el Último Máximo Glacial (UMG) con una temperatura promedio anual (TPA) 4.15°C más fría y una precipitación anual (PA) 1945.94 mm mayor a la actual. En las capas VII-VI la TPA es 3°C mayor con respecto al UMG y la

PA es variable, correspondiendo al Bølling-Allerød. La capa V representa al Younger Dryas con condiciones climáticas similares al UMG. Finalmente, las capas más recientes (IV-I) presentan una TPA similar y una PA inferior a la actual, colocando estas capas posteriores al Holoceno temprano. El uso de la abundancia como un ecométrico para reconstruir el paleoclima resulta una herramienta opcional para conocer los ambientes pasados.

Palabras clave: Centroide de nicho, abundancia, ecométrico, paleoclima, Península de Yucatán.

INTRODUCTION

To study past, present and future of ecological systems is necessary to consider not only their biotic components such as the species, populations, communities, biotic interactions and human activities (Post, 2013) but also to know their abiotic components such as the climate, soil, topography, water temperature, etc. (Birks *et al.*, 2010). All these components help us to reconstruct the paleoclimates and paleoenvironments, thus exploring the ecological theory in past environments, the main objective of the paleoecology (Louys *et al.*, 2012). Paleoclimatic records are essential because they have a main role for understanding the past and present climatic system of the Earth, giving insights to predict the future climate changes (Fitzpatrick *et al.*, 2010).

Generally, paleoclimatic reconstructions have been made using different proxies as rings of trees, glacial records, fossil pollen, oceanic sediments, corals, isotope analysis, foraminifera, ostracods and historic records (Farmer and Cook, 2013). For continental climatic reconstructions it has been use pollen (e.g. Seppä and Bennett, 2003; Correa-Metrio *et al.*, 2012a; Tarasov *et al.*, 2013), glacial records (e.g. Fitzpatrick *et al.*, 2010; Lachniet and Vazquez-Selem, 2005) and packrat middens (e.g. Betancourt *et al.*, 1990).

Vertebrates have ecometrics, defined as functional traits that reflect the interactions among individuals their abiotic surroundings, can be used to reconstruct past climates and environments (Eronen *et al.*, 2010a; Polly *et al.*, 2011). This idea was first proposed by Brattstrom (1956), who established that if past reconstructions are based in a plants-environment relationship, this relationship should also exist for vertebrates allowing to trace past living conditions when we know their current ecological requirements.

Paleoclimatic reconstructions using vertebrates have been done with different ecometrics such as thermal ecology (Markwick 1994, 1998), mass-specific metabolic relationship between body size and climate in poikilotherms (Head *et al.*, 2009, 2013), relationship between ecophysiological groups and the climate (Böhme 2003, 2004, 2008, 2010), transfer functions (Hernández-Fernández y Peláez-Campomanes, 2005), relationship between climate and diversity (Montuire *et al.*, 1997, 2006; Legendre *et al.*, 2005; Escude *et al.*, 2013), hypsodonty patterns (Fortelius *et al.*, 2002, 2006; Eronen *et al.*, 2010b, 2011); mutual climatic range (Blain *et al.*, 2007, 2009, 2010, 2011, 2012, 2013, 2014, 2015; Polly and Eronen, 2011; Smith and Polly, 2013), and taphonomy (Holden *et al.*, 2013). Despite that demographic characteristics are the first to be affected during events of climate change(Davis *et al.*, 1998; Buckley, 2013; HilleRisLambers *et al.*, 2013), paleoclimatic reconstructions with vertebrates have never used species abundance as an ecometric to infer past climates.

According to the center abundance hypothesis, the species reach their highest abundance in the center of their distributional range, declining toward the edges (Brown 1984; Brown *et al.*, 1995; but see Sagarin and Gaines, 2002). This hypothesis has been demonstrated to be noa absolutely true and cannot stated as a general rule (Sagarin and Gaines, 2002), and that alternative patterns of distribution of abundance, such as the ecological niche, should be used (Sagarin and Gaines, 2002, Yañez-Arenas *et al.*, 2012, 2014; Martínez-Meyer *et al.*, 2013; Micheletti and Storfer, 2015; Ureña-Aranda *et al.*, 2015). Yañez-Arenas *et al.* (2012) and Martínez-Meyer *et al.* (2013) developed a method, the Distance to the Niche Centroid approach (DNC), using species distribution models (SDM) to evaluate the relationship between species abundance with their climatic niche. In the present study, we attempt to use the DNC approach and the abundance as a paleoclimatic proxy to reconstruct climatic shifts through different Quaternary stratigraphic layers in the Loltún Cave, Yucatán.

LOCALITY

Loltún Cave, Yucatán

Loltún Cave (20°15’14.35”N, 89°27’20.82”W, 40 m elevation) is located in the southwest portion in the state of Yucatán, México, about 110 km south of Mérida and 7 km southwest from Oxcutzcab (Figure 1). The cave lays in Miocene karstic limestones on the foothills of the Sierra de Ticul. Loltún Cave is an east-west- oriented series of tunnels and chambers. The fossil material here used was obtained in the Huechil chamber that was systematically excavated using a metric grid and controlled stratigraphy between 1977 and 1981 (Arroyo-Cabrales and Álvarez, 1990, 2003; Arroyo-Cabrales and Polaco, 2003). The Loltún Cave is an important archaeological and paleontological site because of the presence of Pleistocene fauna and lithic tools (Arroyo-Cabrales and Álvarez, 2003). Paleontological studies have been focused on mammals (Mercer, 1975; Cope, 1975; Hatt, 1953; Álvarez, 1972; Álvarez and Arroyo-Cabrales, 1990; Arroyo-Cabrales and Álvarez, 1990, 2003), pollen (Xelhuantzi-López, 1986 and Montúfar, 1987), mollusks (Polaco, 1972), birds (Fisher, 1953) and amphibians and reptiles (Langebartel, 1953, Cruz *et al.,* 2016).

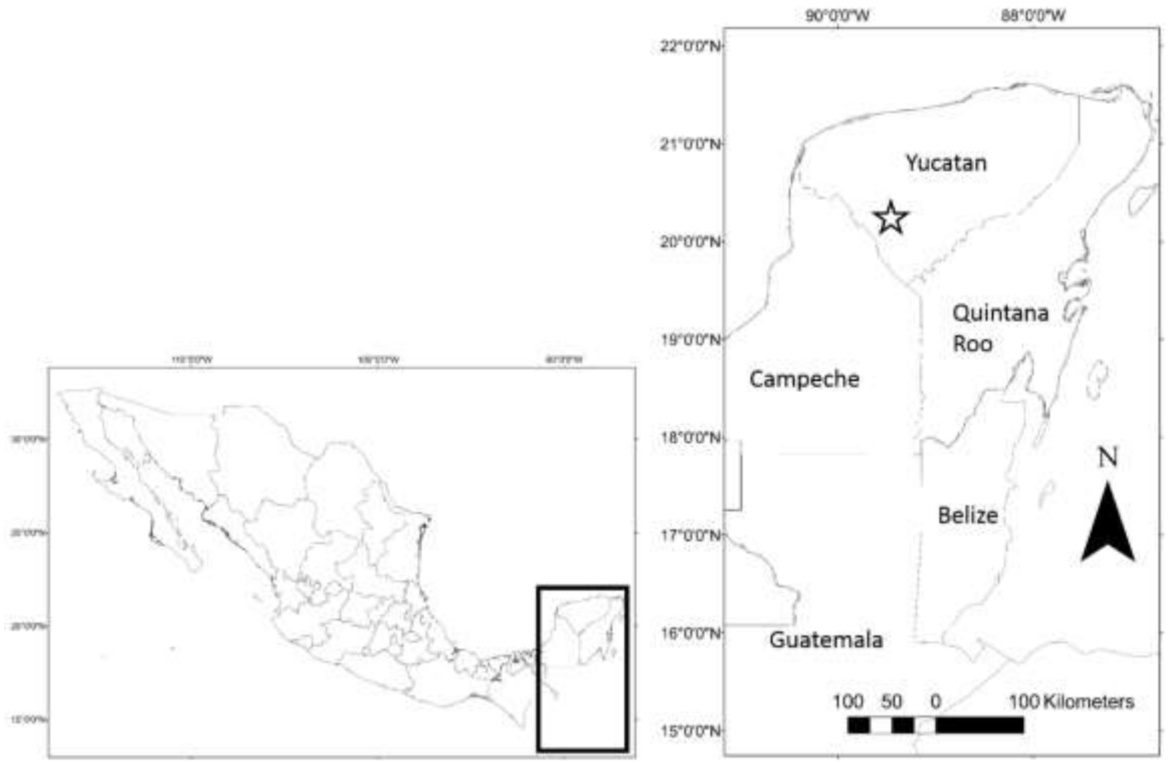

Figure 1. Loltun Cave (White star) in Yucatan Peninsula, Mexico.

The stratigraphic sequence was reported in three main groups (Schmidt, 1988; Arroyo-Cabrales and Álvarez, 2003):

Group 1. Levels I to VII, Ceramic Stage with extinct animals remains are found in the bottom of level VII dated at 12 720 ^{14}C yr BP (15131 ± 289 cal year BP) (Arroyo-Cabrales y Álvarez, 2003).

Group 2. Level VIII, Pre-Ceramic Stage with some lithic elements and extinct fauna.

Group 3. Levels IX to XVI, Pleistocene in age, without any cultural material, but level XI has volcanic ash correlated to the Rosseau tephra dated at 28400 ^{14}C yr BP (32782 ± 296 cal year BP).

MATERIALS AND METHODS

We chose *Cryptotis mayensis* as our species of study because: 1) small mammals are good proxies for paleoclimatic reconstructions (Hernández-Fernández and Peláez-Campomanes, 2005), 2) shrews and moles have the lowest dispersal mean among mammals when climate change occurs (Urban *et al.*, 2013), 3) *C. mayensis* fossil record is well represented in Loltún Cave (Álvarez, 1972; Arroyo-Cabrales and Álvarez, 2003) and 4) we gathered recent data for observed relative abundance of the species in the Yucatán Peninsula (LG *com. pers.*).

Relative fossil abundance

We counted the total number of fossil remains, including the number of identified osteological remains (NISP) and the minimum number of individuals (MNI), which indicates the lowest quantity of fossil organisms represented in each stratigraphic layer (Lyman, 2008). The values of relative fossil abundance were calculated using the MNI of *Cryptotis mayensis* in each stratigraphic layer using the number of cranial remains, right jaws or left jaws.

Current patterns of abundance

Estimation of abundance as a function of the distance niche centroid in the climatic distribution of *Cryptotis mayensis* was done following the method of Yañez-Arenas et al. (2012) and Martínez-Meyer et al. (2013). The species distribution model (SDM) was created using the locality data from natural history collections such as Sistema Nacional de Información sobre la Biodiversidad (CONABIO; www.conabio.org.mx), the Global Biodiversity Information Facility (GBIF; www.gbif.org), the Mammal Networked

Information System (MaNIS; manisnet.org), data reported in literature (Choate, 1970; Woodman and Timm, 1993, 1999; Carraway, 2007; Woodman, 2010, 2011; Guevara *et al.* 2014) and the specimens examined and collected by one of us (LG). The current patterns of abundance of *C. mayensis* were taken from the historical records of the specie and data provided by LG.

The SDM was constructed in MaxEnt v3.3 (Phillips *et al.*, 2006). We used the 19 bioclimatic variables from worldclim`s database (Hijmans *et al*. 2005; www.worldclim.org) with ~1 km of resolution. For the species, 10 distinct models were generated using the *bootstrap* sampling and each model was validated with the 20% of the original records. To evaluate the model, the area under the curve (AUC) generated with the ROC technique (Receiver Operating Characteristic) was used. The potential distribution was obtained by reclassifying with the 10 percentile training presence. This was implemented in ESRI ArcGIS v. 10.0 (Redlands, CA, USA). As a result, it was created a binary map showing the potentially optimal climatic conditions for *C. mayensis* (1 = optimal, 0 = not optimal).

Climatic niche structure

To characterize the climatic niche we used the 19 bioclimatic variables derived from the worldclim database. Each cell of the potential distribution of *C. mayensis* had specific climatic values that were standardized, subtracting each value to its mean and dividing by its standard deviation, producing a z-standard normal variable (0 = mean, 1 = standard deviation) (Yañez-Arenas *et* al., 2012; Martínez-Meyer *et al.*, 2013). Then, we identified the cells with current abundance data and calculated the distance niche centroid (DNC) using the Mahalanobis distance (Yañez-Arenas *et al.*, 2014). The value of the niche centroid is where all the climatic variables are equal to zero (Yañez-Arenas *et* al., 2012).

Using the best fitted regression, in this case the logarithmic regression (Figure 2), we related the current abundance to the distance niche centroid. To calculate the DNC in the past, we converted the relative fossil abundance (MNI) to DNC values. To achieve this, we isolated the x variable from the equation of the logarithmic regression (Table 1).

Paleoclimatic reconstruction

We relate the present DNC with the current mean annual temperature (MAT) and annual precipitation (AP) using the best fit regression. The best fit regression between the DNC and the MAT was a second order polynomial regression (Figure 3a) and between the DNC and AP was a power regression (Figure 3b). This allowed us to find the relationship between the climatic variables and the niche centroid existed. To obtain the paleoclimatic values we isolated the x variable (MAT and AP) (Table 1).

For the relationship between the DNC and the MAT, the second order polynomic regression has two possible results when variable x (MAT) is isolated. We used the x value that involves the negative sign previous to the square root (Table 2), because β_1, the shift parameter, has this sign inside the formula. The β_0 value was not used because it indicates the y-intercept of the curve and β_2 is the rate of curvature (Mendenhall and Sincich, 2015).

The paleoclimatic values inferred for the MAT and the AP for each stratigraphic layer were compared with the climatic records from 1951 to 2010 in the Oxcutzab weather station (smn.cna.gob.mx), Yucatán, the closest weather station to Loltún Cave.

Table 1. Relationship between the abundance and the Distance Niche Centroid (DNC) and between the DNC with regard to the Mean Annual Temperature (MAT) and Annual Precipitation (AP) at present, inside range of *Cryptotis mayensis*. Relationship between the DNC with the abundance, and the MAT and AP with the DNC to estimate the fossil DNC and infer the palaeoclimate of Loltun Cave.

Independent variable (x)	Dependent variable (y)	Regression equation	R^2	Description
DNC	Abundancia	$y = -0.279\ln(x) + 1.2096$	0.1303	Relationship between abundance with regard to DNC.
DNC	Abundancia	$x = e^{\frac{y-1.2096}{-0.279}}$	-	x variable isolated
MAT	DNC	$y = 5.7716x^2 - 295.4x + 3779.7$	0.5043	Relationship between the DNC with regard to MAT.
MAT	DNC	$x = \frac{295.4}{2(5.7716)} - \sqrt{\frac{y}{5.7716}} + \frac{-295.4^2-4(5.7716)(3779.7)}{4(5.7716^2)}$	-	x variable isolated to deduce the palaeotemperature.
AP	DNC	$y = 2 * 10^{-20}x^{6.189}$	0.2101	Relationship between the DNC with regard to the AP.
AP	DNC	$x = \sqrt[6.189]{\frac{y}{2 * 10^{-20}}}$	-	x variable isolated to deduce the palaeoprecipitation.

RESULTS

DNC and abundance of *Cryptotys mayensis* today

The best fit regression between the relative abundance of *Cryptotis mayensis* and the DNC was a logarithmic regression (Figure 2; Table 1). This indicates that today, the highest abundance of the species range in the Yucatán Peninsula is in sites closer to its climatic niche (Figure 3, 4).

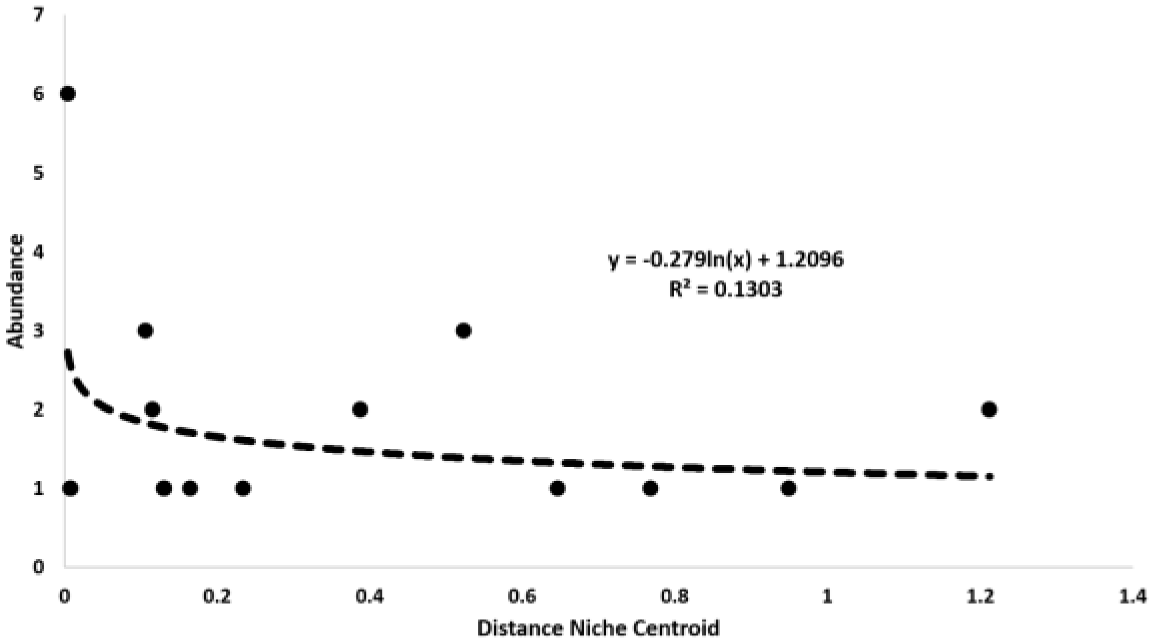

Figure 2. Logarithmic regression between the current relative abundance of *Cryptotis mayensis* and the distance niche centroid today. The specie is more abundant closer to the niche centroid (0).

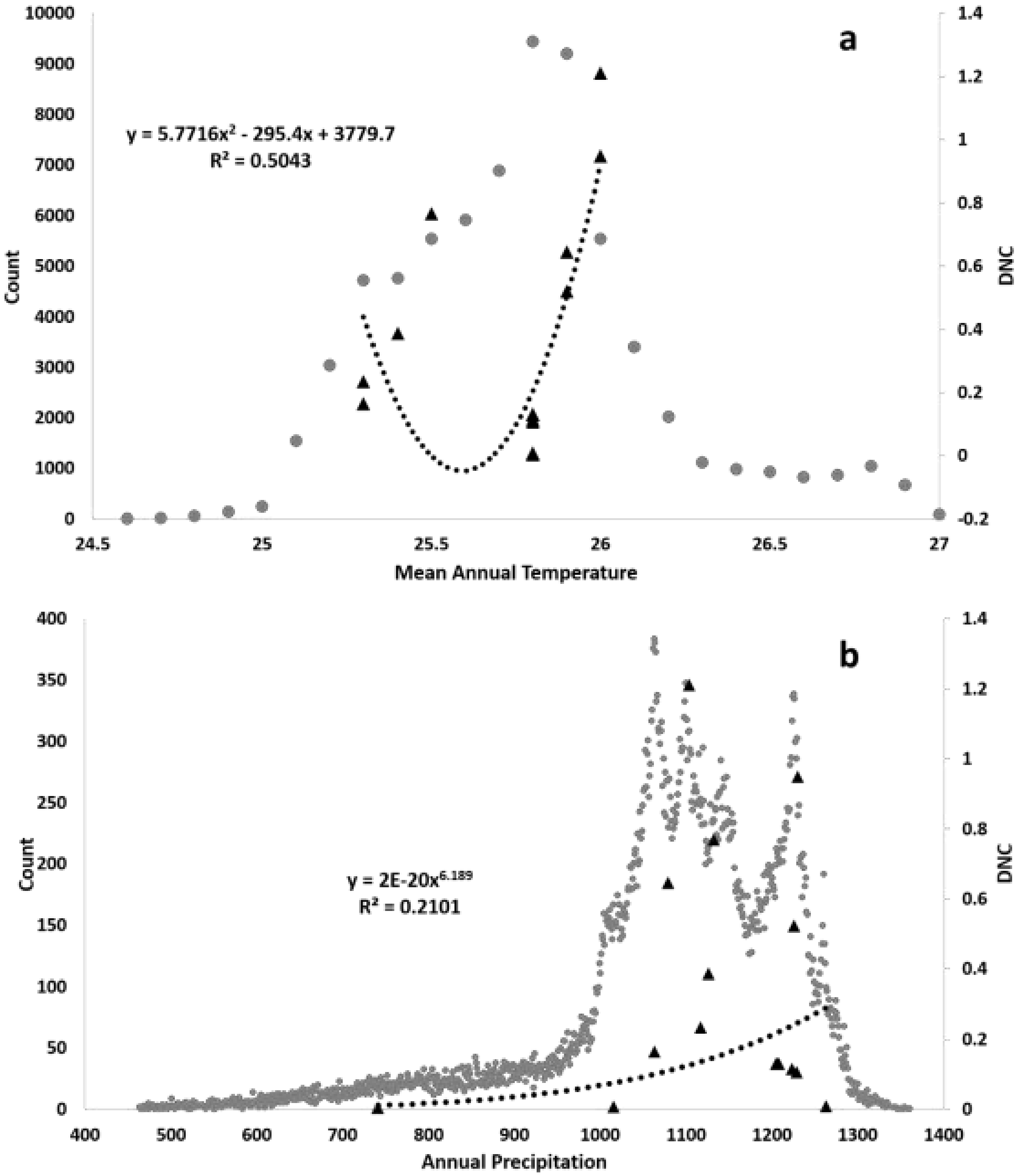

Figure 3. Different regressions between the Distance Niche Centroid (DNC) in relation to a) the Mean Annual Temperature (MAT); and b) the Annual Precipitation (AP) (b). The DNC-abundance ratios are within the MAT and AP values with more cells counts in the *Cryptotis mayensis* distribution.

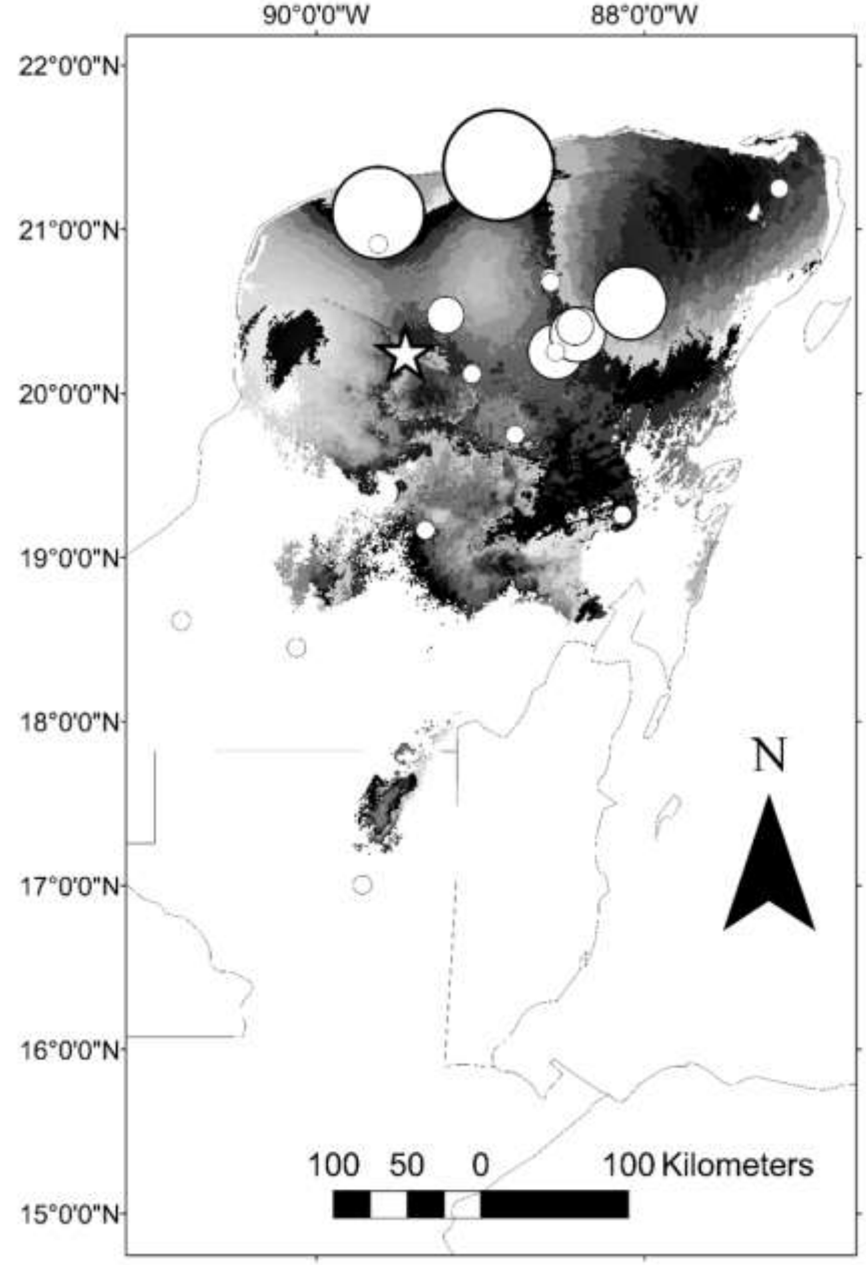

Figure 4. Distance Niche Centroid in the distribuyion range of *Cryptotis mayensis*. Closest values to niche centroid in black and reote values in white. White circles sizes indicate relative abundance value of *C. mayensis* in the sampled sites. White star indicates the location of Loltun Cave.

DNC and relative fossil abundance

A total of 88 fossil remains of *Cryptotis mayensis* were obtained in the different stratigraphic layers (I-XII) of Loltún Cave, Yucatán. The greater relative fossil abundance (MNI) is found in the first layers (I-IV) which are the closest to the Present; we found little abundance in layers V, VII and XII. We did not found fossil remains in layers VI and VIII to XI (Table 3).

Table 3. Number of identified specimens (NISP) and minimum number of individuals (MNI) for each stratigraphic layer (I-XIII) in Loltun Cave.

Layer	Age BP	Left dentaries	Right dentaries	Skulls	NTR	MNI
I	-	5	1	5	11	5
II	-	19	18	20	37	20
III	-	7	9	3	16	9
IV	-	8	11	16	19	16
V	-	0	0	1	1	1
VI	-	0	0	0	0	0
VII	15131	1	2	1	2	2
VIII	-	0	0	0	0	0
IX	-	0	0	0	0	0
X	-	0	0	0	0	0
XI	32782	0	0	0	0	0
XII	-	1	0	0	1	1

The DNC values in the past, obtained for each stratigraphic layer, are closer to zero (niche centroid) when the relative abundance (MNI) is greater (Table 4), as it is observed today.

Paleoclimatic reconstruction

The paleoclimatic reconstruction (Figure 5, Table 4) for the most ancient layer (XII), which is greater than 32782 ± 296 cal year BP, infers a MAT 1.12ºC lower and an AP 596.35 mm higher than today, indicating that the climate was slightly cooler and humid. Anterior to the 32782 ± 296 cal year BP and posterior to the 15131 ± 289 cal year BP (layers X to VIII) the MAT was 4.15ºC lower and the AP was 1945.94 mm greater than the Present, indicating that the climate was colder and more humid. Layer VII, with 15131 ± 289 cal year BP, had a MAT slightly cooler than today (-0.66ºC) and a lower AP (-159.94 mm), indicating that the climate became warmer and drier than layers XII. In layer VI MAT dropped (-1.12ºC) and AP increased (596.35 mm) again to similar conditions found in Layer XII. Layer V present a MAT 4.14ºC lower to the Present and a large increment in the AP of 3069.94 mm, indicating a cold, humid climate, similar to the one found for layer XI-VIII. Most recent layers show the greatest abundance of *C. mayensis* fossil remains, have a slight decrease of the MAT (-0.62) and a large decrease of the AP (-1123.97 to -954.34 mm) when compared to the Present, indicating that the climate was slightly drier with temperatures similar.

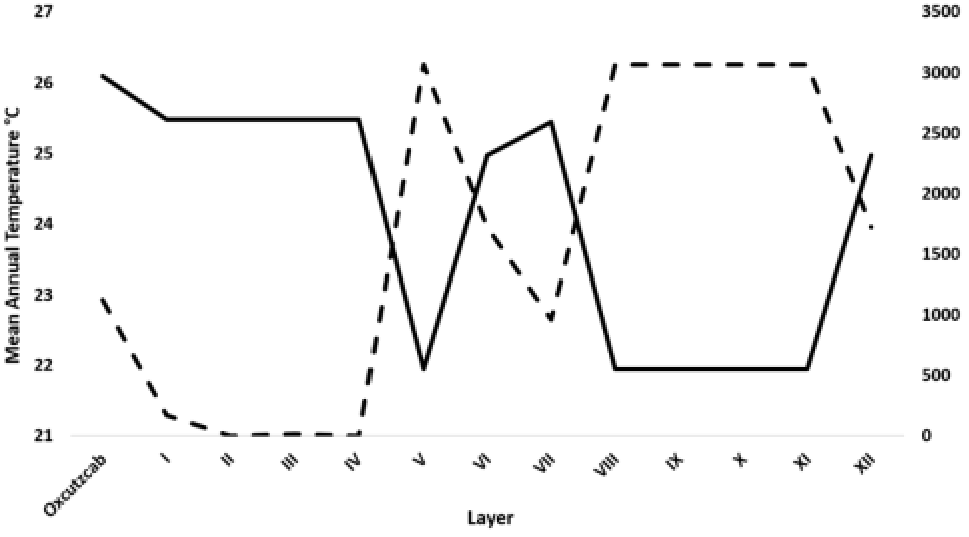

Figure 5. Palaeoclimatic reconstruction of Loltún Cave in each stratigraphic layer. Mean Annual Temperature (Solid line) and Annual Precipitation (dotted line). Interstadial before to 28400 years BP (XII), 28400 years BP (XI), LGM (X-VIII), Bølling-Allerød (VII-VI), Younger Dryas (V), after to Early Holocene (VI-I), Oxcutzcab metereological station nearest to Loltún Cave.

Table 4. Fossil relative abundance, calculated from minimum number of individuals (MNI) and the distance niche centroid (DNC), palaeoclimatic reconstruction to each stratigraphic layer (I-XIII) from Loltún Cave, and contrast with current weather conditions. MAT, Mean Annual Temperature; AP, Annual Precipitation. Interstadial conditions before 32782 ± 296 cal year BP (XII), 32782 ± 296 cal year BP (XI), LGM (X-VIII), Bølling-Allerød (VII-VI), Younger Dryas (V), after Early Holocene (VI-I).

Layer	Age (BP)	MNI	DNC	MAT (°C)	Contrastwith the present (°C)	AP (mm)	Contrastwith the present (mm)
Loltún	Recent	-	-	26.1	0	1124	0
I	-	5	$1.26*10^{-06}$	25.48	-0.62	169.66	-954.34
II	-	20	$5.63*10^{-30}$	25.48	-0.62	0.03	-1123.97
III	-	9	$7.47*10^{-13}$	25.48	-0.62	16.73	-1107.27
IV	-	16	$9.49*10^{-24}$	25.48	-0.62	0.29	-1123.71
V	-	0	76.36	21.95	-4.15	3069.94	1945.94
VI	-	1	2.12	24.98	-1.12	1720.35	596.35
VII	15131	2	0.06	25.45	-0.66	964.06	-159.94
VIII	-	0	76.36	21.95	-4.15	3069.94	1945.94
IX	-	0	76.36	21.95	-4.15	3069.94	1945.94
X	-	0	76.36	21.95	-4.15	3069.94	1945.94
XI	32782	0	76.36	21.95	-4.15	3069.94	1945.94
XII	-	1	2.12	24.98	-1.12	1720.35	596.35

DISCUSSION

DNC and relative fossil abundance

The relationship between the current abundance and the distance niche centroid found for *Cryptotis mayensis,* has also been described for several species of birds, mice, carnivorous animals, monkeys, deers and turtles (Martínez-Meyer *et al.*, 2013; Yañez-Arenas *et al.*, 2014; Manthey *et al.*, 2015; Ureña-Aranda *et al.*, 2015). The best fit equation turned out to be efficient for calculating the DNC of the fossil abundance because, as it is stated in theory, a greater MNI indicated values closer to zero (Yañez-Arenas *et* al., 2012; Martínez-Meyer *et al.*, 2013).

Paleoclimatic reconstruction

Insight of paleoclimatic reconstruction across the stratigraphical layers of Loltún Cave was possible by using the DNC approach of Yañez-Arenas *et al.* (2012, 2014) y Martínez-Meyer *et al.* (2013). Layer XII, the oldest layer before the Last Glacial Maximum (LGM) (>32782 ± 296 cal year BP), indicate a colder and more humid climate than today with a MAT 1.12ºC lower and an AP of 596.35 mm higher than the Present, indicating a colder and more humid climate (Figure 5, Table 4). These results suggest that layer XII represents an interstadial period, where the climate is warmer and less humid than in the LGM (Correa-Metrio *et al.*, 2012a, 2012b; Escobar *et al.*, 2012; Grauel *et al.*, 2016).

Even though we understand that estimations of climate conditions with this method may be flaw when abundance values are cero, we found that cero does have a climatic meaning when comparing to local climate evolution. For layers X to VIII and layer V we did not found any remain of *Cryptotis mayensis.* The absence of this species, locally would mean an estimated temperature of 21.95 °C and a AP of 3069.94 mm, this is 4.15 °C less than today but an AP of 1945.94 mm more than today (Figure 5, Table 4).

For layers X-VIII, between 32782 and 15131 yr BP, the MAT was 4.15ºC lower than the Present and the AP had the greatest increment (1945.94 mm) compared to the Present (Figure 5, Table 4). This results are consistent with the studies for the LGM, which comprises between the 25.6 ka yr BP to the 19 ka yr BP in Titicaca Lake with fossil pollen, isotopes and diatoms (Baker *et al.*, 2001) and in Petén Itzá Lake in Guatemala (Hodell *et al.*, 2008; Bush *et al.*, 2009; Correa-Metrio *et al.*, 2012a, 2012b, 2013; Escobar *et al.*, 2012; Grauel *et al.,* 2016) and Lake Chichancanab in México (Hodell *et al.*, 2012). The MAT during the LGM in these lakes is about 3 to 5ºC colder than the present (Bush *et al.*, 2009; Correa-

Metrio *et al.*, 2012a, 2013). For Lake Titicaca, the precipitation during the LGM shows a great accumulation of water, indicating an increment of the AP (Baker *et al.*, 2001); for Lake Peten Itza all records show, for the LGM, the presence of mesic forest and a more humid climate (Baker *et al.*, 2001; Hodell *et al.*, 2008; Bush *et al.*, 2009; Correa-Metrio *et al.*, 2012a, 2012b; Escobar *et al.*, 2012), being consistet with our data for layers X-VIII.

Layer VII (15131 ± 289 cal year BP) was estimated to be 25.45 °C, this is 0.66 °C less than today and AP was 964 mm, 159.94 mm less than today. In layer VI mAP decreased even more to 24.98 °C, 1.12 °C less than today, but AP increased to 1720.35 mm, 596.35 mm more than today (Figure 5, Table 4). Ours results are consistent with the Bølling-Allerød (14700-12800 yr cal BP) which, posterior to the LGM, presents warmer climatic conditions (Baker *et al.*, 2001; Bush *et al.*, 2009; Correa-Metrio *et al.*, 2012a; Escobar *et al.*, 2012; Hodell *et al.*, 2012) and according to Correa-Metrio *et al.* (2012a), the temperature was 3ºC greater than the LMG as observed in this study. Hodell *et al.* (2008) y Escobar *et al.* (2012) indicated that during the Bølling-Allerød the climatic conditions were humid, while Baker *et al.* (2001), Bush *et al.* (2009) and Correa-Metrio *et al.* (2012a) infer dry conditions. This disagreement was caused by intense climatic oscillation during the Bølling-Allerød (Bush *et al.*, 2009). This explain why in the DNC we obtain more humid values for lauer VII (15131 yr BP) and dryer values for layer VI compated to today; although MAT values were similar.

Similar to what happened in layers VIII-X that belong to the LGM (Figure 5, Table 4), in layer V the MAT has a decrement of 4.15ºC when compared to the present and the AP has an increment of 1945.94 mm. These conditions, that are similar to the LGM and posterior to the Bølling-Allerød, place layers VIII-X in the Younger Dryas (13100-10400 yr BP) which is a cold (Baker *et al.*, 2001; Correa-Metrio *et al.*, 2012a) and humid or dry period (Baketr *et* *al.*, 2001; Correa-Metrio *et al.*, 2012a; Escobar *et al.*, 2012; Hodell *et al.*, 2008; 2012). As it is reported for Lake Titicaca (Baketr *et al.*, 2001) and Lake Petén Itzá (Correa-Metrio *et al.*, 2012a; Escobar *et al.*, 2012), our results shows that there was a decrement in the MAT and an increment in the AP.

For the most recent layers (IV-I), MAT was estimated in 25.48 °C, this is 0.62ºC less than today and AP in 0.29 to 169.66, 1123.71 to 954.34 mm less than today (Figure 5, Table 4) indicating that the period for this layers is the Holocene. From the 10400 yr BP the MAT was similar to the Present (Correa-Metrio *et al.*, 2012a; Hodell *et al.*, 2012), but the climatic conditions were drier after the Early Holocene (10500-8000 yr BP) (Baker *et al.*, 2001; Bush *et al.*, 2009; Correa-Metrio *et al.*, 2012b; Escobar *et al.*, 2012). Our models suggest that climatic conditions of layers IV to I possibly correspond to those posterior to 8000 yr BP. The assignment to time period of a layer by paleoclimatic values has been done previously by Smith and Polly (2013) with mammals in Indiana.

DNC and paleoclimatic reconstructions

Small vertebrates like small mammals, amphibians and reptiles are an efficient paleoclimatic proxy when studying communities (Montuire *et al.*, 1997, 2006; Böhme 2003, 2004, 2008, 2010; Hernández-Fernández and Peláez-Campomanes, 2005; Legendre *et al.*, 2005; Blain *et al.*, 2007, 2009, 2010, 2011, 2012, 2013, 2014, 2015; Polly and Eronen, 2011; Escude *et al.*, 2013; Holden *et al.*, 2013; Smith and Polly, 2013) or their physiological requirements (Markwick 1994, 1998; Fortelius *et al.*, 2002, 2006; Eronen *et al.*, 2010b, 2011; Head *et al.*, 2009, 2013). This study shows that species abundance is a good proxy to infer paleoclimatic reconstructions because the demographic characteristics are the first to be affected during events of climate change (Davies *et al.*, 1998; Buckley, 2013; HilleRisLambers *et al.*, 2013).

The abundance of a species is favoured as long as the climatic conditions are optimal for its development. When these conditions change, the abundance is affected, diminishing it, and if non optimal conditions persist, the species may be driven to extinction (Heino, 2005; VanDerWal *et al.*, 2009; Ureña-Aranda *et al.*, 2015; Bradley, 2016). Using recent records of species abundant records we can calculate the relationship between the abundance and the Distnace Niche Centroid allowing us to use the ecological space of a species and the relative fossil abundance in a locality to reconstruct past climates.

CONCLUSIONS

The abundance of small vertebrate species, as is in *Cryptotis mayensis,* is greater near to the climatic niche centroid. Based on the distance niche centroid theory, small vertebrates abundance can be used as a proxy for paleoclimatic reconstructions when current and fossil abundance records are available.

In Loltún Cave, the oldest layer (layer XII) represent an interstadial before the LGM. During the LGM (layers X-VIII) the temperature was 4.15 ºC colder and the precipitation was 1945.94 mm higher when compared to today, agreeing with reports using other proxies. Layers VII-VI corresponded to the Bølling-Allerød which MAT was 3 ºC higher when compared to the LGM and a variable precipitation along the period. Layer V corresponded to the Younger Dryas with cold and humid climates similar to the LGM. Layers IV-I correspond to a period after the Early Holocene with a MAT similar to the present and a dry period.

Special care needs to be taken when the abundance of a species is cero, in paleontological localities, since absence forbids any reconstruction. We believe, however, fossil abundance equal cero may have a paleoecological interpretation with the methodology described above, if treated in a local o regional scale.

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DISCUSIÓN GENERAL

La Gruta de Loltún (Capítulo I), localizada en la Península de Yucatán, en los estratos XII-XIV con una edad anterior a los 32782 ± 296 cal años AP, muestra una comunidad de anfibios y reptiles pleistocénicos similar a lo encontrado actualmente en la Península de Yucatán, con excepción de *Ctenosaura,* subgenus *Loganiosaura (*Cruz *et al.*, 2016), que se encuentra actualmente en los bosques tropicales de montaña y el bosque tropical lluvioso (Kölher, 2003). Indicando un cambio de distribución de por lo menos 446.4 km al norte de su distribución actual, entre las fases de isótopos marinos (*marine isotope stage,* MIS) 3 y el MIS 2 (Cruz *et al.*, 2016). Esto indicaría cierta concordancia con la hipótesis de estabilidad herpetofaunística durante el Cuaternario, que menciona que durante el Cuaternario en Norte América existió poca extinción o extirpación, así como poca aparición de nuevas especies y pocos cambios en la distribución de los anfibios y reptiles fósiles con respecto al presente (Holman, 1995).

La Cueva de San Josecito en Nuevo León (Capítulo II), con una edad de 32672 ± 1035 cal años AP, indica el cambio de distribución de dos especies de lagartijas y una especie de serpiente. Los datos de la Cueva de San Josecito contradicen la hipótesis de estabilidad herpetofaunística de Holman (1995), contrario a lo observado en la Gruta de Loltún, Yucatán (Capítulo I). Esta hipótesis ya ha sido criticada anteriormente, mostrando cambios importantes en la distribución de anfibios y reptiles durante Cuaternario, comparados con el presente (Blain *et al.*, 2015); y ofreciendo soluciones de cómo identificar restos de anfibios y reptiles del Cuaternario, para no caer en una circularidad biogeográfica (identificar material fósil con material de comparación de las zonas cercanas al sitio fósil únicamente), que permita eliminar una estabilidad no existente (Bell *et al.*, 2010).

Los resultados obtenidos en el capítulo I y II pueden verse afectados por comparar el Presente con un momento en el pasado, por lo que es recomendable estudiar cambios de las comunidades a través del tiempo, en varios momentos entre el pasado y el presente, para entender los procesos de respuesta de los organismos que conforman una comunidad (Magurran *et al.*, 2010; Rull, 2014; Jackson y Blois, 2015; Shimadzu *et al*, 2015; Nuvoloni *et al.*, 2016), como en los capítulos III y IV. Esto se plantea en el presente trabajo con la herpetofauna fósil del Desierto Sonorense (Capítulo III), observando un cambio de la estructura de la comunidad de anfibios y reptiles a través del tiempo, con dos anuros, una lagartija, tres serpientes y dos tortugas que no se encuentran actualmente en la zona, pero en el pasado estaban presentes. Esto contradice la hipótesis de estabilidad herpetológica en el Cuaternario, discutida anteriormente, lo cual seguramente sucedería en la Gruta de Loltún, si se estudiaran las comunidades de anfibios y reptiles a través de varios periodos de tiempo, como se ha observado para mamíferos y moluscos (Álvarez y Polaco, 1982) y murciélagos (Arroyo-Cabrles y Álvarez, 1990) del sitio. La comunidad de anfibios y reptiles en el Desierto Sonorense durante el Cuaternario respondió a los cambios ambientales y climáticos con diferente intensidad, muy similar a lo observado con los mamíferos pequeños durante el Cuaternario en California (Blois *et al.*, 2010).

La estructura de las comunidades de anfibios y reptiles responde a ambos factores, estructura de la vegetación (ambiental) y el clima, sin embargo dilucidar cual es la importancia de cada uno es complicado. El estudio de la herpetofauna del Cuaternario en el Desierto Sonorense (Capítulo III) infiere que el cambio en la estructura de la vegetación es más importante. El estudio de los anfibios y reptiles Pleistocénicos en la Gruta de Loltún (Capítulo I), parece inferir que la estructura de la vegetación también es el más importante, pero no queda muy claro. En cambio, la Cueva de San Josecito (Capítulo II) infiere que tanto la estructura de la vegetación como el cambio climático fueron los causantes de los cambios en la composición herpetofaunística del Pleistoceno. Actualmente, no se sabe cuál de los dos factores influye más en la estructura de las comunidades de vertebrados pequeños, algunos estudios apuntan al clima como el principal factor (Blois y Hadly, 2009; Blois *et al.*, 2010; Blain *et al.*, 2015; Kemp y Hadly, 2016; Royer *et al.*, 2016) y otros a la estructura de la vegetación (Stegner y Holmes, 2013; Rowe y Terry, 2014; Bochaton *et al.*, 2015; Stegner, 2016). De tal manera que queda aún la pregunta sobre cuál es el factor principal que afecta la estructura de las comunidades de anfibios y reptiles o si la intensidad de uno u otro factor se comporta diferente a nivel espacial.

La respuesta de los anfibios y reptiles, así como mamíferos pequeños, a cambios climáticos y/o ambientales a través del tiempo, los hace excelentes indicadores paleoambientales y paleoclimáticos (Brattstrom, 1956; Kay y Maden, 1996; Avery, 2001; Böhme, 2002; Hernández-Fernández y Peláez-Campomanes, 2005; Blain *et al.*, 2007, 2008, 2009; Vieites *et al.*, 2009). Los restos fósiles de anfibios y reptiles de la Gruta de Loltún (Capítulo I) y la Cueva de San Josecito (Capítulo II) tienen una antigüedad similar, muestran disparidad en los cambios ocurridos entre la herpetofauna pleistocénica y actual. Sin embargo, ambos coinciden en que en el Pleistoceno existió una estructura de la vegetación en mosaico, contraria a la vegetación en franjas encontrada actualmente, lo cual se muestra claramente con lo encontrado en el Desierto Sonorense (Capítulo III). Estos cambios en la estructura de vegetación tan marcados entre el Pleistoceno y el Holoceno, se pudieron deber a la extinción de la megafauna, al clima o ambos (Guthrie, 1984; Johnson, 2009a, 2009b; Gill *et al.*, 2009, 2012, 2014; Faith, 2011), permitiendo la presencia de comunidades no análogas a la estructura vegetal, durante el Pleistoceno. Tal como se había predicho con análisis de polen anteriormente (Gill *et al.*, 2009, 2012, 2014; Correa- Metrio *et al.*, 2011, 2012a, 2012b, 2013), se puedieron encontrar diferentes comunidades de fauna actual en el pasado, reunidas en un mismo sitio (Guthrie, 1984). Los cambios en la estructura de la vegetación y de las comunidades de microvertebrados, formando comunidades no análogas en el pasado con respecto al presente, pueden permitir evaluar y predecir futuros cambios de la biota ante efectos de cambio climático y destrucción del hábitat (Veloz *et al.*, 2012; Williams *et al.*, 2013; Rowe y Terry, 2014; Jackson y Blois, 2015; Maguire *et al.*, 2015), utilizando a la paleontología como una herramienta para la conservación en el presente y hacia el futuro (Birks, 2012; Louys, 2012; Stegner y Holmes 2013; Dietl *et al.*, 2015; Dietl, 2016; Kemp y Hadly, 2016).

La respuesta de los microvertebrados (anfibios, reptiles y mamíferos pequeños) a los cambios climáticos en el pasado y en el presente, permiten utilizar la distribución actual de los representantes fósiles como proxy para reconstruir paleoclimas (Blain *et al.*, 2009; Lobo *et al.*, 2016; Lyman, 2016). En la Gruta de Loltún (Capítulo I) los anfibios y reptiles infieren un paleoclima para la edad de 32782 ± 296 cal años AP con una temperatura promedio anual (TPA) 1.47 °C menor y precipitación anual (PA) 85.14 mm de precipitación mayor a la actual, concordando claramente con el registro polínico para la zona de una TPA 1.5 °C menos que el presente y una precipitación menor al Último Máximo Glacial para la zona (Correa-Metrio *et al.*, 2012a, 2012b, Escobar *et al.*, 2012; Grauel *et al.*, 2016).

En la Cueva de San Josecito los reptiles infieren para el Pleistoceno tardío (32672 ± 1035 cal años AP) una TPA de 1 °C menor y una PA de 467 mm mayor a la actual. Los reptiles indican que la precipitación es mayor durante el Pleistoceno tardío con respecto a la actual, esto también se ve reflejado en los trabajos de paleoprecipitación en el norte de México (Roy *et al.*, 2013) concordando con nuestros datos. El problema se encuentra en la inferencia de la TPA para esta época en la Cueva de San Josecito, aunque los dos indican la presencia de un interestadial para la zona, concordando con los registros de Groenlandia (Rahmstorf, 2002; Ahn y Brook, 2013) y sedimentos marinos (Rashid y Boyle, 2007; Alvarez-Solas *et al.*, 2010; Lynch-Stieglitz *et al.*, 2014), así como con la Gruta de Loltún en Yucatán (Capítulo I), los valores de la temperatura no concuerdan con los 5-6 °C menos que lo actual para la zona (Metcalfe, 2006). Sin embargo, Cruz (2012) utilizando la distribución de anfibios y reptiles juntos, para la misma edad en la Cueva de San Josecito, encontró que los valores de TPA 5.97°C son menores a los actuales y una precipitación 95.96 mm mayor a la actual, concordando perfectamente para lo que se conoce con otros proxies en el norte de México (Metcalfe, 2006; Roy *et al.*, 2013). Esto sugiere que se utilicen los anfibios y reptiles juntos para inferir paleoclimas por medio del intervalo climático mutuo, y que presentan mejores resultados que si se analizan los grupos por separado.

La reconstrucción paleoclimática para el Desierto Sonorense utilizando anfibios y reptiles, por medio del método de intervalo climático mutuo dio buenos resultados a lo largo de los diferentes periodos de tiempo (Capítulo III). Siendo congruente con lo que se ha encontrado con otros proxies como polen fósil (McAuliffe y Van Devender, 1998; Metcalfe, 2006; Barron *et al.*, 2012), espeleotemas (Antiano y McDonald, 2013), superficie de la temperatura del océano (Barron *et al.*, 2012), registros geoquímicos (Roy *et al.*, 2012, 2013, 2014; Kirby *et al.*, 2013), foraminíferos (Poore *et al.*, 2005). Esto hace que el método de intervalo climático mutuo utilizando vertebrados pequeños sea bueno para determinar paleoclimas (e.g. Blain *et al.*, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016; López-García *et al.*, 2011, 2013, 2014, 2015, 2016), aunque se deben tomar precauciones a la hora de realizarlo (Lobo *et al.*, 2016) y conocer bien las bases del método (Lyman 2016).

Finalmente, proponemos un método alternativo para reconstruir paleoclimas con vertebrados utilizando la relación de abundancia con el centroide del nicho climático (Capítulo IV). En caso de no tener un sitio con buena representación fósil a nivel comunidad, se puede utilizar la abundancia de un taxón, ya que las características demográficas son las primeras en verse afectadas durante eventos de cambios ambientales y climáticos (Davis *et al.*, 1998; Blois y Hadly, 2009; Buckley, 2013; HilleRisLambers *et al.*, 2013). Parte fundamental de este método es conocer cómo se comportan las poblaciones de un taxón a lo largo de la distribución actual, lo cual también es una desventaja, porque en México se conoce muy poco de ecología de poblaciones para anfibios y reptiles (e.g. Yañez-Arenas *et al.*, 2014, 2016; Ureña-Aranda *et al.*, 2015), así como de los vertebrados pequeños. Sin embargo, si se cuentan o se realizan los trabajos de demografía, se puede utilizar el método de centroide de nicho climático, para conocer la relación entre el clima y la demografía de una especie (Martínez-Meyer *et al.*, 2013; VanDerWal *et al.*, 2009; Ureña-Aranda *et al.*, 2015; Bradley 2016; Searcy y Shaffer, 2016; Weber *et al.*, 2016) y así poder utilizar el método para reconstruir el paleoclima, como se realizó para la Gruta de Loltún, en Yucatán (Capítulo IV). La TPA inferida, para la capa XII con más de 32782 ± 296 cal años AP, es de 1.12 °C, muy similar a lo encontrado con el método de intervalo climático mutuo utilizando herpetofauna (1.5 °C), lo cual concuerda también con los datos que se tienen con otros proxies como el polen fósil para la zona (Correa-Metrio *et al.*, 2012a, 2012b, Escobar *et al.*, 2012; Grauel *et al.*, 2016). Con el método de abundancias y centroide de nicho se pudo inferir el paleoclima de diferentes estratos, mostrando concordancia en la reconstrucción paleoclimática con otros proxies como registros polínicos (Hodell *et al.*, 2008, 2012; Bush *et al.*, 2009; Correa-Metrio *et al.*, 2012a, 2012b, 2013; Escobar *et al.*, 2012; Grauel *et al.*, 2016), diatomeas e isótopos (Baker *et al.*, 2001), de diferentes sedimentos lacustres. Se recomienda explorar este método para otros sitios y otros grupos de organismos en la reconstrucción paleoclimática.

CONCLUSIONES GENERALES

Comparando las comunidades de anfibios y reptiles durante el Pleistoceno y el Holoceno, de diferentes sitios de México, se encontró que existen cambios en la distribución de las especies comparándolas con el Presente, demostrando que la hipótesis de estabilidad herpetológica durante el Cuaternario no es aplicable en el país o debe tomarse con mucho cautela.

La respuesta de las comunidades de anfibios y reptiles, a través del tiempo, responde a los cambios en la estructura de la vegetación y a los cambios climáticos.

Los anfibios y reptiles, así como otros vertebrados pequeños, son buenos proxies paleoambientales y paleoclimáticos, para reconstruir condiciones ambientales y climáticas del pasado.

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