

## Article

# Paleoclimatic Reconstruction Based on the Late Pleistocene San Josecito Cave Stratum 720 Fauna Using Fossil Mammals, Reptiles, and Birds

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**Abstract:** Advances in technology have equipped paleobiologists with new analytical tools to assess the fossil record. The functional traits of vertebrates have been used to infer paleoenvironmental conditions. In Quaternary deposits, birds are the second-most-studied group after mammals. They are considered a poor paleoambiental proxy because their high vagility and phenotypic plasticity allow them to respond more effectively to climate change. Investigating multiple groups is important, but it is not often attempted. Biogeographical and climatic niche information concerning small mammals, reptiles, and birds have been used to infer the paleoclimatic conditions present during the Late Pleistocene at San Josecito Cave (~28,000 <sup>14</sup>C years BP), Mexico. Warmer and dryer conditions are inferred with respect to the present. The use of all of the groups of small vertebrates is recommended because they represent an assemblage of species that have gone through a series of environmental filters in the past. Individually, different vertebrate groups provide different paleoclimatic information. Birds are a good proxy for inferring paleoprecipitation but not paleotemperature. Together, reptiles and small mammals are a good proxy for inferring paleoprecipitation and paleotemperature, but reptiles alone are a bad proxy, and mammals alone are a good proxy for inferring paleotemperature and precipitation. The current paleoclimatic results coupled with those of a previous vegetation structure analysis indicate the presence of non-analog paleoenvironmental conditions during the Late Pleistocene in the San Josecito Cave area. This situation would explain the presence of a disharmonious fauna and the extinction of several taxa when these conditions later disappeared and do not reappear again.

**Keywords:** paleoecology; paleoenvironmental reconstruction; ecological niche modelling; Quaternary; Mexico



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## 1. Introduction

Starting in the 1980s [1], technological advances in computational power, modeling, and databases have equipped paleobiologists with new tools to analyze the fossil record [2]. Furthermore, the field of paleobiology has demonstrated that it can provide long-term perspectives on the impacts of climate change on natural systems [3]. Accordingly, it is possible to conduct studies of paleoclimatic reconstructions using different data and approaches. For example, recent studies have used different proxies, such as ice cores, sediments, speleothems, pollen, tree rings, and corals, to reconstruct climate during the Quaternary [4].

Plants and animals have responded in different ways to past and ongoing climate change [5]. Species may exhibit functional traits or ecometrics that enable inferences concerning climatic differences at different temporal and geographical scales [6–9]. In vertebrates, tooth crown height (hypsodonty) correlates with precipitation, relationships between body size and temperature, thermal ecology, community diversity, and biogeographical information. These correlations are used to make paleoclimatic inferences [8,10]. Mammals and reptiles are the groups most commonly used for paleoclimatic reconstruction [8,10]. Amphibians, fish, and birds are used infrequently. In American Quaternary deposits, birds are the second-most-studied group after mammals, but they are seldom used in paleoclimatic reconstructions. They are considered a poor paleoambiental proxy because of their high vagility and phenotypic plasticity that allows them to respond more effectively to climate change [11–14].

In Mexico, more than 20 cave excavations have occurred, but very few have controlled stratigraphy, radiometric dates, or small vertebrate studies [15]. Only recently have quantitative paleoenvironmental (including paleoclimate) reconstructions of the Mexican Pleistocene been conducted using vertebrates. The ecometrics that were first used, and which are still most commonly used with Mexican vertebrates, are stable isotopes on megafaunal remains [16,17]. Paleoenvironmental reconstructions, however, are usually very similar: some mammals have grazer diets, others have browser diets, and still others are mixed feeders. Together, they imply a grassland with open forests. Stable isotopes have not been used with fossil mammals from caves. The questions are what kind of forests were those open forests, and what was the paleoclimate? Microvertebrates are suitable proxies that can be used to reconstruct past environments and, thereby, answer these questions [10,18,19], and caves are excellent places to find their preserved remains. In this study, the paleoclimatic conditions in the Mexican Late Pleistocene are inferred based on distributional and climatic niche information concerning different groups of vertebrates (i.e., small mammals, squamate reptiles, and birds) found in San Josecito Cave. The effectiveness with which the paleoclimate can be reconstructed using each group is compared in order to generate the most reliable reconstruction.

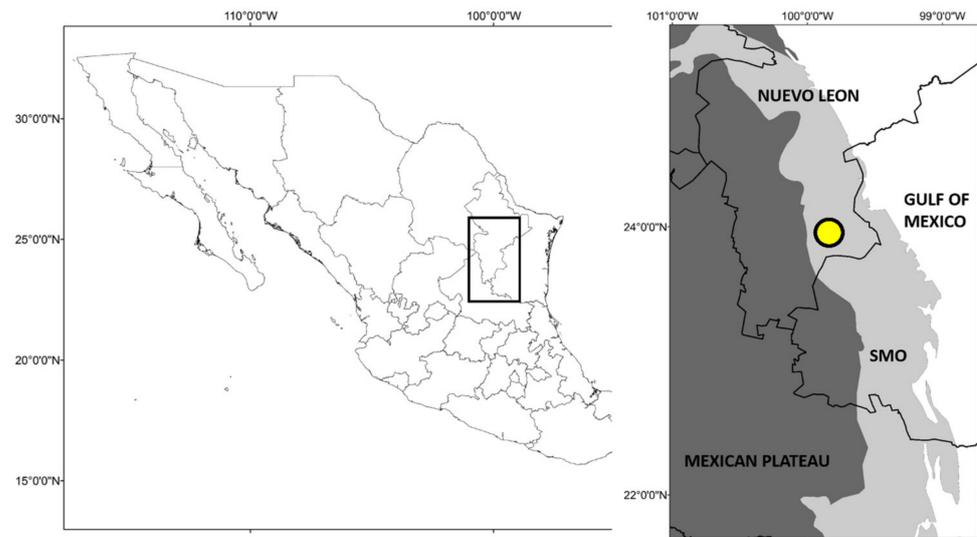
## 2. Materials and Methods

### 2.1. Study Area

San Josecito Cave is located on the western flank of the Sierra Madre Oriental, 1 km SSW of Ejido de San Josecito and 8 km SW of Arramberry (23°57'21'' N, 99°54'45'' O, 2250 m elevation) in Northeast Mexico (Figure 1). The cave is a single fissure with multiple entrances formed by Late Jurassic or Early Cretaceous folded limestone. Today, three natural entrances lead down vertically from 12 m to 30 m into a main cavity. None of the entrances provide easy access to the cave today, and they most likely did not in the past. Because a walking or horizontal entrance does not exist, the cave probably has acted as a natural trap. The single cavity measures 34 m long and 25 m wide, and it narrows to the north [20–22]. Several successive faunas are present within a stratigraphic framework, dating from 45,000 to 11,000 <sup>14</sup>C years BP [20].

### 2.2. Material

Information is used about the fossil small mammals, reptiles, and birds previously identified from stratum 720 (Table 1; [22]) radiocarbon dated to 28,005 ± 1035 <sup>14</sup>C years BP (32,942 ± 4077 calendar years). The Nearest Living Relative (NLR) is utilized for the fossil taxa identified. If the identified fossil species still exists, then the biogeographical and ecological information of this species (e.g., *Pluvialis* cf. *P. squatarola* = NLR *Pluvialis squatarola*) is employed. If it is an extinct species, the information about the closest species or genus (e.g., extinct *Desmodus stocki* = NLR *Desmodus rotundus*) is applied.



**Figure 1.** Location of San Josecito Cave (yellow circle) in the Sierra Madre Oriental (SMO), Nuevo León, Mexico.

**Table 1.** Stratum 720 (~28,000 <sup>14</sup>C years BP/~32,900 calendar years) fossil taxa from San Josecito Cave utilized in the paleoclimatic reconstruction.

Group	Orden	Familia	Especie			
Birds	Accipitriformes	Accipitridae	<i>Aquila chrysaetos</i>			
		Galliformes	Phasianidae	<i>Cyrtonyx montezumae</i>		
		Gruiformes	Rallidae	<i>Rallus limicola</i>		
		Charadriiformes	Charadriidae	<i>Pluvialis</i> cf. <i>P. squatarola</i>		
		Strigiformes	Strigidae	<i>Megascops asio</i> / <i>M. kennicottii</i> <i>Asio otus</i> <i>Ciccaba virgata</i>		
	Passeriformes	Corvidae		<i>Gymnorhinus cyanocephalus</i> <i>Corvus corax</i> <i>Sturnella</i> sp. <i>Barisia ciliaris</i> <i>Barisia imbricata</i>		
			Reptiles	Squamata	Icteridae	<i>Phrynosoma modestum</i> <i>Phrynosoma orbiculare</i> <i>Sceloporus</i> spp. <i>Tantilla</i> sp. <i>Heterodon</i> cf. <i>H. simus</i> <i>Hypsiglena</i> <i>Storeria</i> sp.
					Anguidae	
					Phrynosomatidae	
					Colubridae	
Mammals	Soricomorpha	Viperidae	<i>Crotalus</i> spp.			
		Soricidae	<i>Sorex altoensis</i>			
		Chiroptera	Phyllostomidae	<i>Desmodus stocki</i> <i>Leptonycteris nivalis</i> <i>Myotis californicus</i> <i>Myotis thysanodes</i>		
			Vespertilionidae			
	Rodentia	Cricetidae		<i>Microtus mexicanus</i> <i>Neotoma albigula</i> <i>Neotoma albigula</i> <i>Peromyscus difficilis</i> <i>Peromyscus labecula</i> <i>Peromyscus levipes</i> <i>Reithrodontomy megalotis</i>		
			Lagomorpha	Leporidae	<i>Sylvilagus floridanus</i>	

### 2.3. Occurrence Data

Presence data were obtained for the NLR from the Global Biodiversity Information Facility (GBIF) [23] for the American continent. Specimens preserved, occurrence, and material sample were included. Cleaning the occurrence data was performed using the R packages Wallace 2.0 [24] and NicheToolBox [25]. The database was cleaned by removing records that: (1) were less than 5 km away (because the resolution of the climate layers is of 2.5 arc min (~4.5km)); (2) fell into the sea; or (3) were outside of the known range distribution. For all taxa distribution, the International Union for Conservation of Nature (IUCN [26]) geographic range information was used. For birds, information was obtained from BirdLife International [27]. For some reptiles, distribution information published in the scientific literature was applied [28–36] because it contained more detailed information about the distribution of those taxa.

### 2.4. Potential Distribution Maps

All species modeled in this work are endemic to North America. This region is used as a background area to estimate potential geographical distribution for each species using ecological niche modeling approaches [37]. Ecological niche models (ENMs) have been fitted with eight algorithms: multivariate adaptive regression spline (mars); boosted regression trees (gbm); random forest (rf); classification and regression trees (cart); support vector machines (svm); flexible discriminant analysis (fda); generalized linear model (glm); and generalized additive model (gam) using the *sdm* R package [38]. To calibrate the models, pseudo-absences have been used that were generated based on three-times the number of presences for each species using the *ecospat.rand.pseudoabsences* function from the *ecospat* R package [39]. This procedure has maximized the number of pseudo-absences for model validation using standard validation metrics [40,41]. An ensemble model has been used to generate a potential geographical distribution where models were weighted according to a high value of the True Skill Statistic metric (TSS [41]). The continuous outputs maps have been converted into binary maps (i.e., presence and absence) using the 10th percentile training presence threshold.

### 2.5. Paleoclimatic Reconstruction

The Mutual Ecogeographic Range (MER) method [10] was used to reconstruct the Late Pleistocene paleoclimate based on the stratum 720 fauna from San Josecito Cave with modification when using the ENM to obtain the potential distribution [42–46]. The overlapping area was obtained between the distribution for each vertebrate group and combining the groups. That is, the overlapping areas of all small mammals, all reptiles, and all birds were found. Next, the overlapping area combining mammals and reptiles was determined and then the area combining all groups (small mammals, reptiles, and birds). The overlap between the distributions of taxa was determined using QGIS 3.16 software [47]. The climatic variables mean annual temperature (bio01, MAT) and annual precipitation (Bio12, AP) from worldclim database 2.0 [48] were extracted from the overlapping area for each taxa combination area using *extract* function from the raster R package [49]. The results then were compared with their current values obtained from the Meteorological Station 00019066 General Zaragoza (<https://smn.conagua.gob.mx/>, Servicio Meteorológico Nacional de México, accessed on 30 March 2022) that is the nearest station to the San Josecito Cave area.

## 3. Results

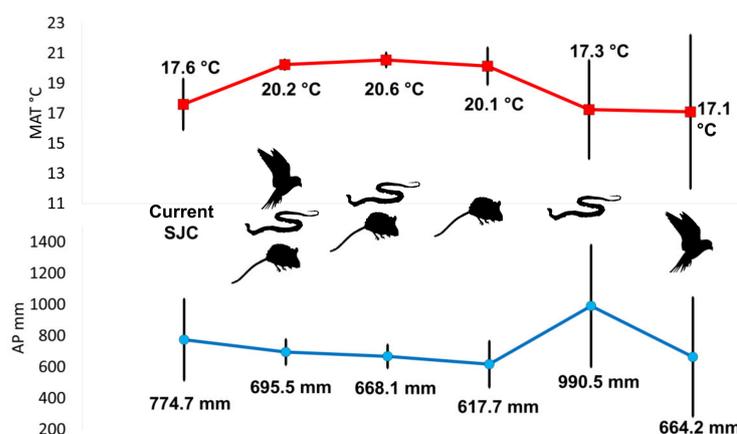
### 3.1. Paleoclimatic Inferences of the Late Pleistocene from San Josecito Cave

Different vertebrate groups provide different paleoclimatic information (Table 2 and Figure 2), and not all groups are useful in inferring paleotemperature, paleoprecipitation, or both by themselves. A community is a set of species that occurs at a determinate time and geographical space, and its assemblage of species has to pass a series of environmental filters to be present [50]. The climatic data of all groups, therefore, have been utilized to

reconstruct the paleoclimatic values for the Late Pleistocene from San Josecito Cave (Table 2 and Figure 2). The all-vertebrates group information becomes a point of comparison to evaluate the paleoclimatic inferences from each group of vertebrates. The paleotemperature inference using the all-vertebrates group indicates a warmer (+2.64 °C) mean annual temperature (MAT = 20.24 °C). The paleoprecipitation is dryer (−79.175 mm) with an annual precipitation (AP = 695.5 mm) with respect to the present (Table 2 and Figure 2).

**Table 2.** Paleoclimatic reconstruction of the Late Pleistocene based on San Josecito Cave using the all-vertebrates community and the difference with respect to the current climate in the San Josecito area. The results obtained with all vertebrates are compared with small mammals and reptiles together and small mammals, reptiles, and birds separately.

	MAT °C (Average ± SD)	AP mm (Average ± SD)
Current San Josecito Cave	17.6 ± 1.69	774.68 ± 259.85
Difference	0	0
All vertebrates	20.24 ± 0.32	695.5 ± 80.95
Difference	+2.64	−79.175
Mammals and reptiles	20.55 ± 0.48	668.1 ± 74.18
Difference	+2.95	−106.58
Mammals	20.14 ± 1.22	617.7 ± 147.66
Difference	+2.54	−156.98
Reptiles	17.25 ± 3.27	990.5 ± 389.77
Difference	−0.35	+215.82
Birds	17.1 ± 5.1	664.2 ± 380.87
Difference	−0.5	−110.48

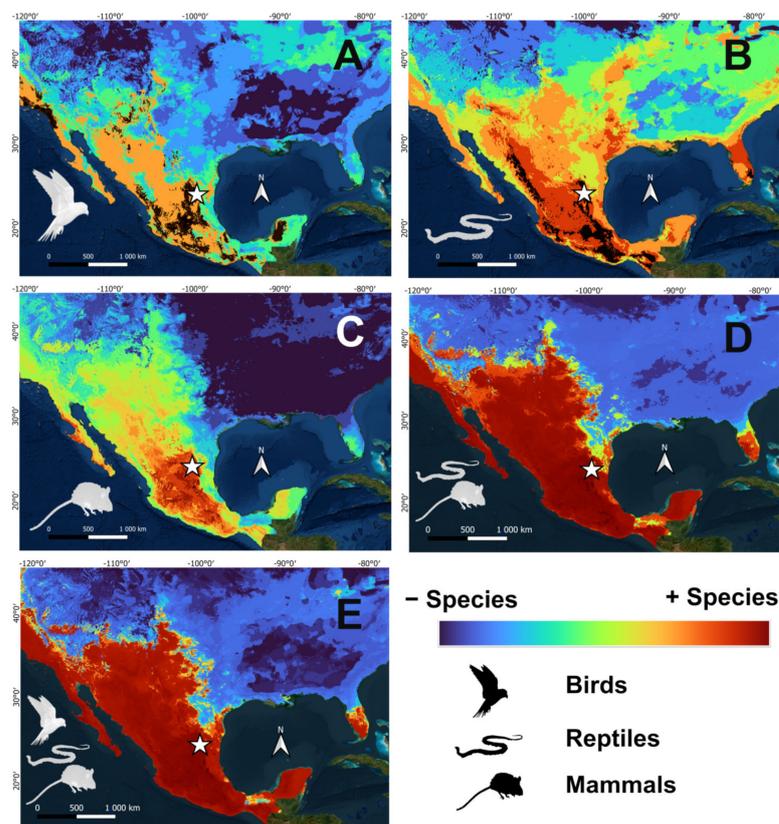


**Figure 2.** Paleoclimatic reconstruction from San Josecito Cave (SJC), stratum 720 assemblage community. The paleoclimatic reconstruction from San Josecito Cave with the different groups of vertebrates including the mean annual temperature (MAT, red squares) and annual precipitation (AP, blue circles) are compared with the current climate at the fossil locality. The paleoclimatic values inferred with the all-vertebrate community were used to reconstruct the paleotemperature and precipitation of the Late Pleistocene from San Josecito Cave.

### 3.2. Paleoclimatic Inferences between Vertebrate Groups

The overlap area with the optimal climatic conditions was determined for each vertebrate group (Figures 3 and 4) that would facilitate the development of the stratum 720 assemblage community. The birds presented the largest overlap area, encompassing the Veracruz, Chihuahuan, Sierra Madre Occidental, Sierra Madre del Sur, Pacific Lowland, and Yucatán provinces [51,52]. The reptiles had an overlap area composed of the Austroriparian, Sierra Madre Oriental, Sierra Madre Occidental, Transmexican Volcanic Belt, Sierra Madre del Sur, and Chiapas Highlands [51]. The small mammals exhibited the least overlap area, consisting of the Sierra Madre Oriental and Sierra Madre del Sur [51]. The overlap area

using small mammals and reptiles together contained only the Sierra Madre Oriental province [51] in San Luis Potosí State in Cerritos, Río Verde, Cárdenas, and Ciudad Maíz area. The overlap area using all vertebrates together comprised the Sierra Madre Oriental province [51] in San Luis Potosí State, with a smaller area of only the Cárdenas and Ciudad Maíz area.



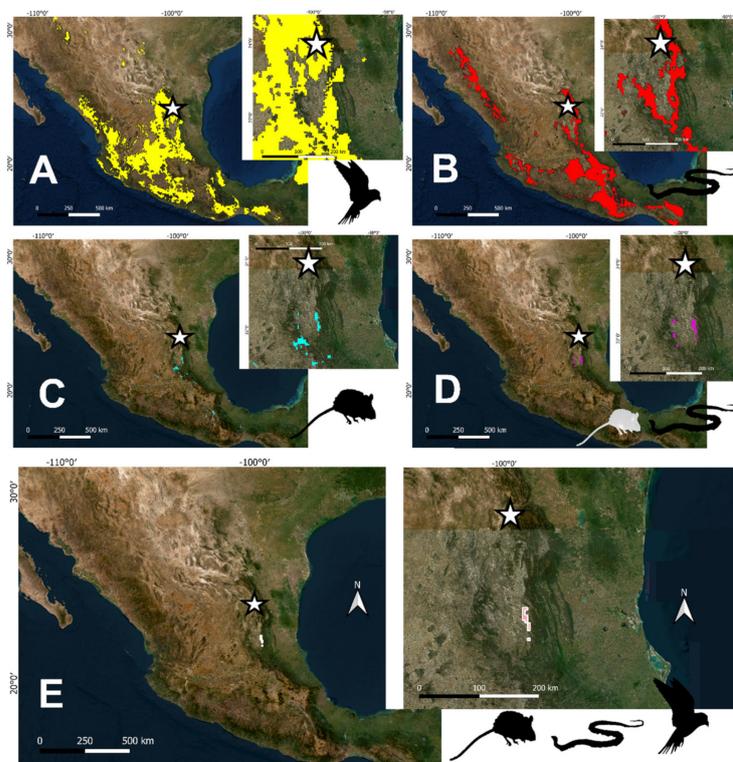
**Figure 3.** Mutual Ecogeographic Range analyses showing the overlap areas where optimal climatic conditions exist for all Nearest Living Relative (NLR) species of birds (A), reptiles (B), small mammals (C), the community of reptiles and small mammals (D), and all-vertebrates community (E) are present. San Josecito Cave is represented by the white star.

Birds and reptiles infer a slightly cooler MAT ( $-0.5\text{ }^{\circ}\text{C}$  and  $-0.35\text{ }^{\circ}\text{C}$ , respectively), contrary to that found using the all-vertebrates group (Table 2 and Figure 2). These two groups show the highest variation from the average of the data. For San Josecito Cave, these groups are a poor proxy on their own to infer paleotemperature in the Late Pleistocene. Small mammals indicate a warmer MAT ( $+2.54\text{ }^{\circ}\text{C}$ ), similar to that found using the all-vertebrates group, and exhibit the least variation from the average of the data (Table 2 and Figure 2). Small mammals, then, are a good proxy on their own to infer paleotemperature in the Late Pleistocene at San Josecito Cave.

Regarding annual precipitation, the reptiles infer the highest precipitation value (AP = 990.5 mm) with respect to the present (Table 2 and Figure 2). This value overestimates the precipitation values found using the all-vertebrates group and is the highest variation from the average. These findings indicate that reptiles are a poor proxy on their own to infer Late Pleistocene paleoprecipitation at San Josecito Cave. Birds and mammals individually have similar precipitation values (AP = 664.2 mm and 617.7 mm, respectively) and imply a dryer condition than today during the Late Pleistocene in the San Josecito Cave area. This finding is similar to that found using all vertebrates (Table 2 and Figure 2). The difference between the small mammals and bird groups is that small mammals show a smaller variation with respect to the average of the data and birds a higher variation.

This situation indicates that the small mammals on their own are a better proxy to infer paleoprecipitation during the Late Pleistocene in the San Josecito Cave area but that birds on their own are an acceptable proxy.

Paleoenvironmental inferences using herps and small mammals together are known from the literature [22,43,44,53–65]. The paleoclimatic reconstruction obtained with the all-vertebrates group is compared with respect to using the reptile and small mammal results. The combined small mammals and reptiles infer the warmest MAT (+2.95 °C) and driest (AP = −106.58 mm) conditions with respect to the present (Table 2 and Figure 2). Paleotemperature and paleoprecipitation are similar to those inferred by small mammals alone rather than reptiles alone, but the variation in the data is reduced almost to that of the all-vertebrates group (Table 2 and Figure 2). This situation indicates that a combined small mammal and reptiles group is a good proxy for paleoclimatic reconstruction for San Josecito Cave. A comparison of small mammals and reptiles together versus birds alone shows that paleoprecipitation values are similar between these two groups. This finding underscores that birds are an acceptable proxy for paleoprecipitation at San Josecito Cave.



**Figure 4.** Overlap areas with the optimal climatic conditions so that all Nearest Living Relative (NLR) taxa of birds (A), reptiles (B), small mammals (C), the community of reptiles and small mammals (D), and all-vertebrates community (E) are present. The small mammals, small mammals and reptiles community, and all-vertebrates community inferred the more reliable current climate conditions in the San Josecito Cave area today. San Josecito Cave is represented by the white star.

#### 4. Discussion

##### 4.1. Paleoclimatic Inferences between Vertebrate Groups

San Josecito Cave is one of the best-studied Late Pleistocene localities in Mexico, with six new fossil species, eight extinct birds, and nineteen extinct mammals [22]. San Josecito Cave exhibits a disharmonious biota that could have been maintained by equable climates with reduced seasonal extremes that have no modern analogs [22]. Paleoenvironmental studies have been undertaken with birds [66], reptiles [67], and an all-vertebrates approach [22], the latter being the only one with a quantitative inference. Paleoclimatic recon-

structions, however, have not been made previously with the San Josecito Cave assemblages.

For stratum 720 (~28,000  $^{14}\text{C}$  years BP/~32,900 calendar years), a paleotemperature (MAT = 20.24 °C) warmer (+2.64 °C) and paleoprecipitation (AP = 695.5 mm) dryer (−79.175 mm) are inferred with respect to the present (Table 2 and Figure 2). These paleoclimate data are in agreement with those found by Van Devender [68] for the lowest, hottest elevations in the Chihuahuan Desert, with warmer and drier climates during the Middle Wisconsin (45,600–24,100 years BP). The warmer temperature found in this study is consistent with pollen and diatom analyses in Central Mexico that indicate an interstadial period during MIS 3 (56,000–35,000 years BP), with warmer conditions with respect to the present [69,70]. The Late Pleistocene dry conditions at San Josecito Cave are in agreement with the driest conditions during the MIS 3 interstadial (~40,000–31,000 years BP) obtained with speleothem geochemical proxies in Cueva Bonita [71] located 99.7 km SE of San Josecito Cave. The concordance of the paleoclimatic inference in this study with other proxies reflects that the presence of the various taxonomic groups within the same site/stratigraphic unit contains the information of all environmental filters those species have had to pass to be present in a determinate time and geographical space [50].

Previous paleoenvironmental inferences for San Josecito Cave with birds from a mixed assemblage across stratigraphic units indicate the presence of a mixture of forest/woodland, grassland, and wetland [66]. Reptiles infer drier conditions than today, with a subhumid climate and a more marked winter season [67]. In the most recent study, a coniferous-oak forest similar to the Rocky Mountains biome was noted but with a non-analog vegetational association that includes grassland. A drier and cooler (by 2 °C) climate than today is suggested using small mammals, reptiles, and birds [22]. The current results are concordant with a drier condition but not with a cooler climate. This contrast between vegetation structure (coniferous-oak forest) and climate (drier and warmer) in the past indicates the presence of non-analog paleoenvironmental conditions during the Late Pleistocene in the San Josecito Cave area. This situation would explain the presence of the stratum 720 disharmonious fauna and the extinction of several taxa when these conditions disappear and do not reappear later.

#### 4.2. Paleoclimatic Inferences between Vertebrate Groups

The use of birds in paleoclimatic reconstruction is very limited because they are considered a poor paleoambient proxy. They have high vagility and phenotypic plasticity, allowing them to respond more effectively to climate change [11–14]. In this analysis, however, birds are a good proxy for inferring paleoprecipitation but not for mean annual paleotemperature. Some bird populations today are affected by summer temperature and precipitation but not by mean annual temperature [72]. Further, the Late Pleistocene stratum 720 San Josecito Cave birds have been used in quantitative paleoenvironmental reconstructions [22]. In that study, the birds inferred a different component of the paleoenvironment (grasslands, wetlands) with respect to reptiles and small mammals (coniferous and oak forest). Other recent studies where birds provide qualitative paleoenvironmental information are for North America [73], the Neotropics [74–76], Europe [77–79], and South Africa [80].

In this study, small mammals and reptiles together are a good paleoclimatic proxy. This situation also has been the case for the Iberian Peninsula [53–65], Mexico [22,43], and Argentina [44]. In these cases, the paleoclimatic reconstructions are in agreement with other proxies, such as pollen, isotopes, diatoms, and soils studies. While small mammals and reptiles together are a good paleoclimatic proxy, when only reptiles were used in this study, they are a poor proxy to infer paleotemperature and paleoprecipitation. Most likely, the small mammals–reptiles group is a good proxy in this study because the overlap area of this group is similar to that of the all-vertebrates group (Figure 4).

Although reptiles depend on external heat sources to regulate their body temperature, climate is a key factor influencing the distribution and abundance of species [81–84].

Paleoprecipitation reconstructions are always subject to large uncertainties [10,85]. Other studies, however, infer that the richness of Palearctic reptiles is highly correlated with precipitation [86], and most reptile species are highly sensitive to precipitation tolerances [83]. The identification of half of the reptile taxa at the genus level may be the reason that the San Josecito Cave stratum 720 reptiles were a poor proxy. This observation is important in relation to the quality of reconstructions. At the genus level and higher, ecological niches appear relatively resistant to climatic change, even as pronounced as glacial–interglacial transitions [87]. Climate factors have a greater effect at the species level [87]. These findings explain why the stratum 720 small mammals at San Josecito Cave are a good proxy, because all fossils were identified to species level. This aspect underscores the importance, then, of identifying remains to the species level to the extent possible and using all vertebrates identified to the species level in paleoclimatic reconstructions.

The biogeographical and climatic niche information of modern vertebrates in paleoclimatic reconstruction has been used previously for North America [42,44,46,88]. This globally applicable method is a good tool to infer the paleoenvironmental reconstruction in vastly different parts of the world, such as Europe [10,89–91] and South America [43]. It is, however, the first time that this method has been used to incorporate birds. The use of climatic niche and biogeographical information can be particularly helpful in inferring paleoclimatic conditions if other types of proxies (e.g., pollen, diatoms, glacial records, isotopes) are not available.

## 5. Conclusions

A warmer (+2.64 °C) mean annual temperature (MAT = 20.24 °C) and a drier (−79.175 mm) annual precipitation (AP = 695.5 mm) are inferred with respect to the present for the Late Pleistocene at San Josecito Cave using the fossil stratum 720 (~28,000 <sup>14</sup>C years BP/~32,900 calendar years) vertebrate assemblage. The inferences are based on a combined approach of small mammals, reptiles, and birds. The all-vertebrates community approach has been used because all groups represent the assemblage of species that pass a series of environmental filters to be present in the past at San Josecito Cave. Individually, different vertebrate groups provide different paleoclimatic information. When an all-vertebrates group is used, variation in the data is reduced, and paleoclimate reconstructions are more reliable.

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