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Paleoclimatic reconstruction of the Late Pleistocene Talara Tar Seeps, Peru, using fossil reptiles, small mammals, and birds

J. Alberto Cruz [a,b,*], Emily L. Lindsey [a,c,d]

[a] La Brea Tar Pits and Museum, 5801 Wilshire Boulevard, Los Angeles, CA 90036, USA
[b] Centro de Investigación Quinametzin, Coordinación Nacional de Arqueología, Instituto Nacional de Antropología e Historia, Córdoba 45, Mexico City 06700, Mexico
[c] Department of Earth Sciences, University of Southern California, 3651 Trousdale Pkwy, Los Angeles, CA 90089, USA
[d] Institute of the Environment and Sustainability, University of California, 619 Charles E Young Dr E #300, Los Angeles, CA 90024, USA

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ABSTRACT

Functional traits of vertebrates can be used to infer paleoenvironmental conditions, allowing research into past climate changes and biotic responses. Birds are generally considered poor palaeoclimatic proxies due to their high vagility. Here, we analyze biogeographical and climatic niche information from multiple vertebrate groups including small mammals, reptiles, and birds to infer the paleoclimatic conditions present during the Late Pleistocene (~14,500–17,000 years BP) at Talara, an asphaltic paleontological locality on the northern Peruvian coast. We created Ecological Niche Models for the nearest living relative of each fossil species identified at Talara. We then used the Mutual Ecogeographic Range method, obtaining the overlapping area between distributions for each vertebrate group (birds, reptiles, and small mammals) as well as for combinations of groups, to infer the paleoclimate at Talara and to determinate what taxonomic groups are best for reconstructing climate in this system. Our analyses indicate that conditions at Talara were slightly cooler and significantly wetter than those of the present day. Individually, different vertebrate groups provide different paleoclimatic information. Birds were found to be a poor paleoclimatic proxy. Mammals were good for inferring paleoprecipitation but not paleotemperature. Reptiles were good group for inferring paleotemperature but not paleoprecipitation. While analyzing all vertebrate groups together yields the most robust conclusions, reptiles and small mammals combined are a good proxy for inferring both paleoprecipitation and paleotemperature. Our results suggest an interstadial period that agrees with paleotemperatures inferred from isotopic and sedimentary information. Our research indicates that today, the southern portion of the Cauca biogeographic province (230 km NE from Talara) has comparable climatic conditions to Late Pleistocene Talara. Understanding how the Talara region transitioned from this biodiverse ecosystem to the hyperarid coastal desert of today could have important implications for predicting biotic response and tipping points in the context of modern climate change.

1. Introduction

Palaeobiological studies are useful tools for ecologists because they can provide a unique perspective on biotic responses to past environmental changes, giving insight into the history of the Earth as well as modern global change (Kiessling et al., 2023). The Quaternary period (2.58 million years ago to present) is a particularly useful focus for such studies, as it is the closest in time and biogeographical conditions to our current situation and most Quaternary species are the same as, or closely related to, those living today. Importantly, the Quaternary is characterized by colder (glacial) and warmer (interglacial) periods, allowing comparison with the no-analog greenhouse world of the near future (Jackson and Williams, 2004).

In the Americas, the Quaternary period was relatively stable geologically, without significant orographic events that affected the continental conformation, thus constraining inferences about the impact of paleoclimatic change on ecosystem structure and function. Moreover, humans arrived in the Americas during the Late Pleistocene, giving scientists the opportunity to compare ecosystem structure before and after human presence (Elias, 2013) in order to better understand anthropogenic impacts on past and present organisms.

Historically, much Quaternary paleontological focus in the Americas has been on large vertebrates (e.g. Lemon and Churcher, 1961; Agenbroad, 1978; Stock, 2001; Fariña et al., 2013; Arroyo-Cabrales and

* Corresponding author at: La Brea Tar Pits and Museum, 5801 Wilshire Boulevard, Los Angeles, CA 90036, USA.
E-mail addresses: cruzsilvajac@yahoo.com.mx (J.A. Cruz), elindsey@tarpits.org (E.L. Lindsey).

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Manzanilla-López, 2022), but as these species tend to have large ranges and broad environmental tolerances, they are of limited utility for understanding the paleoclimatic history of a site (Ramstein et al., 2021, Le Verger, 2023). On the other hand, studies of much more ecologically sensitive small vertebrates can be leveraged for quantitative paleoclimatic reconstruction (Blain et al., 2018, and references herein). The Mutual Ecogeographic Range (MER) analysis is a quantitative technique that involves overlying the current distributions of all taxa found in a paleontological locality to infer climate conditions in the past (Blain et al., 2008, Faith and Lyman, 2019). The MER and Ecological Niche Models (ENM) have been combined to infer paleoclimatic conditions in United States (Smith and Polly, 2013), Mexico (Cruz et al., 2016, 2021a, 2023; Hernández-Hernández et al., 2020; Medina-Castañeda et al., 2022), and Argentina (Cruz et al., 2021b).

Despite the utility of microvertebrate based ENM as a paleoecological tool, so far its application in Neotropical paleontological sites has been rare (Cruz et al., 2016, 2021a, 2023; Arroyo-Cabrales et al., 2021; Medina-Castañeda et al., 2022). In South America, only two vertebrate-based paleoclimate reconstructions have been published: Kay and Madden (1997) found significant positive correlations between the functional characteristics of 16 recent and one fossil nonvolant mammal faunas and precipitation in the Miocene of La Venta, Colombia; and Cruz et al. (2021b) inferred a colder and drier climate in the Late Pleistocene to Middle Holocene and a change to warmer and humid climate during the Late Holocene using MER and ENM in small and medium size mammals and reptiles at Cueva Tixi, Argentina. Increasing the number of paleoclimatic reconstructions for South America is important: today, this region is home to high biodiversity that is disproportionately threatened by modern climate change (Girardello et al., 2019; Powers and Jetz, 2019), and understanding how climate change has affected past Quaternary biotic communities in this region can help scientists and conservation practitioners make better decisions to mitigate its impacts today (Barnosky et al., 2017, Ramstein et al., 2021, Kiessling et al., 2023).

A challenge for conducting paleoclimate reconstructions using microvertebrates is a collection bias towards larger vertebrates, which are more commonly preserved and discovered, and are rarely found at the same localities as small ones. One exception are asphaltic deposits ("tar pits"), which can accumulate and preserve large and small fossils as well as a variety of biotic tissues (bone collagen, plant cellulose, insect chitin, and shell carbonates) (Templeton, 1964; Woodard and Marcus, 1973; Harris, 2015; Lindsey and Seymour, 2015; Holden et al., 2017; Mychajliw et al., 2020). Tropical South America has several such deposits including Inciarte and Orocual in Venezuela (Solórzano et al., 2015; Ruiz-Ramoni et al., 2022); La Carolina, Coralito, and Tanque Loma in Ecuador (Lindsey and Lopez, 2015; Lindsey and Seymour, 2015;

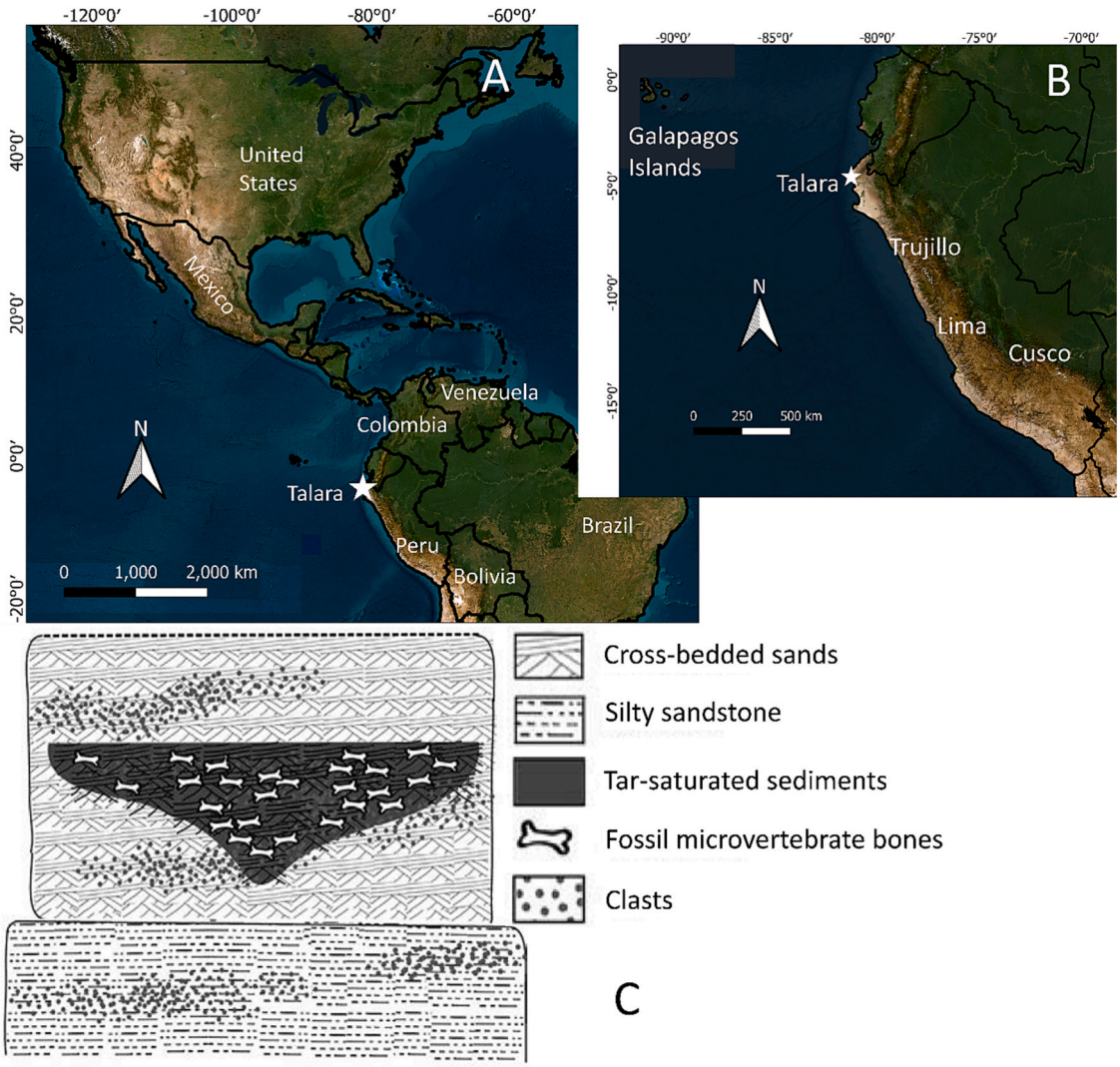

Fig. 1. Location of Talara Tar Seeps (white star) in South America (A), Northern Perú (B) with the stratigraphy in "Tablazos" shape (C). Fig. C modified from Lindsey and Seymour (2015).

Mychajliw et al., 2020); and Pampa La Brea ("Talara") in Perú (Lemon and Churcher, 1961; Seymour, 2015). The richest and best studied of these sites is Talara (Lindsey and Seymour, 2015), and several publications have identified microvertebrates in addition to the more well-studied megafauna. In this study, we use MER and ENM to infer the Pleistocene paleoclimatic conditions at Talara using reptile, bird and small mammal taxa reported from this site.

2. Study area

Talara is located at 4°38′38.92″ S, 81°8′9.47″ W, about 120 m above sea level (Fig. 1). The asphalt seeps occur in Pleistocene terraces ("Tablazos") that overlie Paleogene oil-bearing rocks (Lemon and Churcher, 1961; Seymour, 2015; Moretto et al., 2017; Deza et al., 2019). As at other global tar pit sites, regional tectonic activity creates areas of structural weakness, allowing crude from these rocks to seep to the surface, where it forms sticky pools capable of trapping small and large vertebrates, invertebrates, and windborne plant material (Lemon and Churcher, 1961; Lindsey and Seymour, 2015). Over time, these pools build up with fluvial and/or aeolian input, eventually becoming buried when the seep activity ceases; the asphaltic fossil-bearing sediments occur as numerous, isolated lenticular deposits up to 2 m deep x 10 m wide. Preliminary radiocarbon dating of preserved plant material (including some inferred to represent megafaunal gut contents or coprolite) and insects from several Talara deposits has yielded a narrow time range for the Talara locality between ~14,500–17,000 years before present (Lindsey et al., 2022).

The Talara site was excavated in 1958 and 1961 by personnel from the Royal Ontario Museum (ROM, Toronto, Canada), which houses more than 28,000 vertebrate specimens from these excavations (Seymour, 2015). More recent collections have been made by the Instituto de Paleontologìa at the Universidad Nacional de Piura, Perú in 2003 and 2007 (Moretto et al., 2017). Megafaunal taxa identified from the site include the canid *Aenocyon dirus*; the felids *Smilodon fatalis, Panthera onca,* and *Puma concolor;* ungulate species *Odocoileus virginianus*, *Paleolama aequatorialis,* and *Equus* cf. *E. santaeelenae*; the gomphothere *Notiomastodon platensis*; the large rodent *Neochoerus* sp.; and the xenarthran taxa *Holmesia occidentalis, Eretmotherium laurillardi, Glossotherium tropicorum,* and *Catonyx chiliense* (Lindsey and Seymour, 2015; Seymour, 2015). Other taxa identified include medium and small mammals (in particular the sechuran fox *Dusicyon sechurae*), reptiles, amphibians, numerous birds, and insects of the orders Coleoptera, Lepidoptera, and Orthoptera (Seymour, 2015).

3. Material and methods

We compiled taxonomic lists of fossil birds, reptiles, and small- and medium-sized mammals from Talara from previously published sources including: Campbell (1979), Czaplewski (1990) Lindsey and Seymour (2015), Seymour (2015), Oswald and Steadman (2015), Moretto et al. (2017), and Deza et al. (2019). For each fossil taxon, we determined the Nearest Living Relative (NRL), i.e. the most closely-related extant species of the fossil taxa (e.g. extinct *Gymnogyps howardae* = NLR *Gymnogyps californianus*) or the genus (e.g. extinct *Conepatus talarae* = NLR *Conepatus*) (Table 1). We then obtained the biogeographical and ecological information for each NLR.

3.1. Occurrence data

We obtained occurrence data for each NLR from the Global Biodiversity Information Facility (GBIF, 2022) for the American continent (North and South America, Central America and Caribbean). We included the categories *specimens preserved, occurrence, material sampled*, and in cases where more presence data was required, we included *human observation* and *machine observation*. We excluded *fossil presence* data because this analysis uses recent ecological information of the species to project it into the past. We cleaned the database removing records that were less than 5 km apart (because the resolution of the climate layers is of 2.5 arc min [~4.5 km]), records that fell in the ocean, and records that were outside of known range distributions. For all taxon distributions we used the geographic range information from IUCN (2022) and in the case of birds, we included information from eBird (Sullivan et al., 2009; eBird, 2021). For some reptiles and mammals, we used species distribution information published in scientific literature (Weber and Gonzalez, 2003; Meaney et al., 2006; Williams and Genoways, 2007; Albino and Carlini, 2008; Rosen and Herrmann, 2008; Clavijo and Ramírez, 2009; Cossíos, 2010; Velazco and Cadenillas, 2011; Esser et al., 2013; Moreira et al., 2013; de Oliveira and Moura, 2013; Schiaffini et al., 2013; Sales et al., 2014; Marín-Vasquez et al., 2015; Ribeiro-Júnior, 2015; Ruete and Leynaud, 2015; Kehlmaier et al., 2017; Ribeiro-Junior and Amaral, 2017; Sobral-Souza et al., 2017; Suárez-Atilano et al., 2017; de Andrade et al., 2018; Nigenda-Morales et al., 2018; Reynolds and Henderson, 2018; Carvalho et al., 2019; Mandujano and Reyna-Hurtado, 2019; Loaiza et al., 2020; Bezerra-Santos et al., 2021; Falcón Espitia and Jerez, 2021; Rhodin et al., 2021; García Bravo et al., 2022) because these publications provide more detailed information about the distributions of some taxa.

3.2. Distribution maps

We created an ENM for the NLR of each fossil taxon identified at Talara. We used the ENM because it is necessary to model the environmental conditions where a species *can* live even if the species has not been found in the modeled areas (Soberón et al., 2017). We used the *clean presence* data for each taxon and the 19 bioclimatic variables from Worldclim 2 (Fick and Hijmans, 2017) with a resolution of 2.5 min arc (~4.5 km) for the entire American continent. We used this region as our calibration area because we have NLR taxa in our study with modern distributions only in North America (e.g. *Gymnogyps californianus*), only in South America (e.g. *Dicrodon*), and in both North and South America (e.g. *Didelphis* sp.). To avoid autocorrelation between the climatic variables we used the R package NicheToolBox (Osorio-Olvera et al., 2020). We chose the variables with a correlation greater than 0.85 for the American continent, using the climatic variables bio01 (annual mean temperature), bio02 (mean diurnal range), bio03 (Isothermality), bio05 (max temperature of warmest month), bio07 (temperature annual range), bio08 (mean temperature of wettest quarter), bio09 (mean temperature of driest quarter), bio12 (annual precipitation), bio14 (precipitation of driest month), bio15 (precipitation seasonality), bio18 (precipitation of warmest quarter), bio19 (precipitation of coldest quarter). We ran the Maxent 3.4.4 software (Phillips et al., 2006, 2017) using the R packages Wallace 2.0 (Kass et al., 2022), with all features classes (linear, quadratic, hinge, product); 30% of the presence data points used as test points; 10,000 background points; regularization multiplier = 1, and clamping = off. We performed 30 models for each NLR taxon and chose the model with the highest value below the curve area and the lowest omission rate value (Fig. 2). To obtain species maps with the suitable areas, we converted the continuous output maps into a binary map (1 = suitable, 0 = unsuitable) using the *10 percentile training presence* threshold.

3.3. Paleoclimatic reconstruction

We used the MER (Blain et al., 2008, 2016, 2018) and ENM (Cruz et al., 2016, 2021a, 2021b, 2023; Hernández-Hernández et al., 2020; Medina-Castañeda et al., 2022) to infer the Late-Pleistocene paleoclimate of Talara, Peru, and evaluated the reliability of individual microvertebrate groups as paleoecological indicators. We obtained the overlapping area between the distribution for each of the vertebrate groups (NLR mammals, NLR reptiles, and NLR birds) as well as the overlapping area combining NLR mammals and NLR reptiles and combining all the groups (NLR mammals + NLR reptiles + NLR birds).

Table 1
Fossil taxa identified from the Late Pleistocene Talara Tar Seeps and their Nearest Living Relatives (NRL). We exclude extinct taxa where the NRL is the family level. † = extinct species. [a]Campbell (1979), [b]Czaplewski (1990), [c]Lindsey and Seymour (2015), [d]Seymour (2015), [e]Oswald and Steadman (2015), [f]Moretto et al. (2017), and [g]Deza et al. (2019).

Clase	Orden	Familia	Especie	NLR
Reptiles	Crocodylia[d]	Alligatoridae	*Caiman crocodilius*	*C. crocodilius*
	Squamata[d]	Boidae	*Boa* sp.	*Boa*
		Phylloactylidae	*Phyllodactylus* sp.	*Phyllodactylus*
		Iguanidae	*Iguana* sp.	*Iguana*
		Gymnophthalmidae	*Cercosaura* sp.	*Cercosaura*
		Teiidae	*Callopistes* sp.	*Callopistes*
			Dicrodon sp.	*Dicrodon*
	Testudines[g,d]	Emydidae	*Trachemys* sp.	*Trachemys*
		Geoemydidae	*Rhinoclemmys* sp.	*Rhinoclemmys*
		Testudinidae	*Chelonoides* sp.	*Chelonoides*
Mammals	Didelphimorphia[c,d]	Didelphidae	*Didelphis* sp.	*Didelphis*
			Marmosa sp.	*Marmosa*
	Chiroptera[b,d,f]	Phyllostomidae	*Lophostoma* cf. *L. occidentale*	*L. occidentale*
			Lophostoma silvicolum	*L. silvicolum*
		Vespertilionidae	*Eptesicus innoxius*	*E. innoxius*
			Eptesicus sp.	*Eptesicus.*
			Lasiurus egregius	*L. egregius*
			Myotis sp.	*Myotis.*
	Rodentia[c,d]	Hydrochoeridae	†*Neochoerus* sp.	*Hydrochoerus hydrochaeris*
	Carnivora[c,d]	Canidae	*Lycalopex sechurae*	*L. sechurae*
		Felidae	*Leopardus* sp.	*Leopardus*
		Mustelidae	†*Conepatus talarae*	*Conepatus*
	Artiodactyla[c,d]	Cervidae	*Mazama* sp.	*Mazama*
		Tayassuidae	*Pecari tajacu*	*P. tajacu*
Aves	Tinamiformes[a,d]	Tinamidae	*Crypturellus* cf. *C. transfasciatus*	*C. transfasciatus*
	Anseriformes[a,d]	Anatidae	*Dendrocygna autumnalis*	*D. autumnalis*
			Chloephaga melanoptera	*C. melanoptera*
			Cairina moschata	*C. moschata*
			†*Anas talarae*	*Anas*
			†*Anas amotape*	*Anas*
			†*Anas sanctaehelenae*	*Anas*
			Anas bahamensis	*A. bahamensis*
			Nomonyx dominicus	*N. dominicus*
	Galliformes[a,d]	Cracidae	*Penelope* cf. *P. purpurascens*	*P. purpurascens*
	Podicipediformes[a,d]	Podicipedidae	*Tachybaptus dominicus*	*T. dominicus*
			Podilymbus podiceps	*P. podiceps*
	Ciconiiformes[a,d]	Ciconiidae	*Jabiru mycteria*	*J. mycteria*
			Mycteria americana	*M. americana*
	Pelecaniformes[a,d]	Ardeidae	*Ardea cocoi*	*A. cocoi*
			Ardea alba	*A. alba*
			Egretta thula	*E. thula*
			Egretta caerulea	*E. caerulea*
			Egretta sp.	*Egretta*
			Syrigma sanctimartini	*S. sibilatrix*
			Nycticorax nycticorax	*N. nycticorax*
		Threskiornithidae	†*Eudocimus peruvianus*	*Eudocimus*
			Eudocimus albus	*E. albus*
			†*Theristicus wetmorei*	*Theristicus*
			Platalea ajaja	*P. ajaja*
	Accipitriformes[a,d]	Cathartidae	*Coragyps* cf. *C. atratus*	*C. atratus*
			Cathartes aura	*C. aura*
			†*Gymnogyps howardae*	*G. californianus*
			Vultur gryphus	*V. gryphus*
			†*Sarcoramphus? fisheri*	*S. papa*
		Accipitridae	*Buteogallus terrestris*	*Buteogallus*
			Parabuteo unicinctus	*P. unicinctus*
			Geranoaetus polyosoma	*G. polyosoma*
			Geranoaetus melanoleucus	*G. melanoleucus*
			Buteo sp.	*Buteo*
	Gruiformes[a,d]	Rallidae	*Porzana carolina*	*P. carolina*
	Charadriiformes[a,d]	Burhinidae	*Burhinus superciliaris*	*B. superciliaris*
		Charadriidae	*Pluvialis squatarola*	*P. squatarola*
			Pluvialis dominica	*P. dominica*
			Charadrius collaris	*C. collaris*
			Charadrius semipalmatus	*C. semipalmatus*
			Charadrius vociferus	*C. vociferus*
		Thinocoridae	*Thinocorus rumicivorus*	*T. rumicivorus*
			†*Thinocorus koepckeae*	*Thinocorus*
		Jacanidae	*Jacana spinosa*	*J. spinosa*
		Scolopacidae	*Actitis macularius*	*A. macularius*
			Tringa solitaria	*T. solitaria*
			Tringa melanoleuca	*T. melanoleuca*

(*continued on next page*)

Table 1 (*continued*)

Clase	Orden	Familia	Especie	NLR
			Tringa semipalmata	*T. semipalmata*
			Tringa flavipes	*T. flavipes*
			†*Tringa ameghini*	*Tringa*
			Numenius cf. *N. borealis*	*N. borealis*
			Arenaria interpres	*A. interpres*
			Calidris himantopus	*C. himantopus*
			Calidris minutilla	*C. minutilla*
			Calidris melanotos	*C. melanotos*
			Calidris mauri	*C. mauri*
			Caldris chapmani	*Caldris*
			Phalaropus tricolor	*P. tricolor*
			†*Phalaropus graui*	*Phalaropus*
		Laridae	*Leucophaeus atricilla*	*L. atricilla*
			Leucophaeus pipixcan	*L. pipixcan*
	Columbiformes[a,d]	Columbidae	*Zenaida asiatica*	*Z. asiatica*
			Zenaida auriculata	*Z. auriculata*
			Columbina talpacoti	*C. talpacoti*
			Columbina cruziana	*C. cruziana*
	Strigiformes[a,d]	Tytonidae	*Tyto alba*	*T. alba*
		Strigidae	*Bubo virginianus*	*B. virginianus*
			Athene cunicularia	*A. cunicularia*
			Asio flammeus	*A. flammeus*
	Caprimulgiformes[a,d]	Caprimulgidae	*Chordeiles acutipennis*	*C. acutipennis*
		Caprimulgidae	†*Caprimulgus piurensis*	*Hyropsalis and Antrostomus*
	Falconiformes[a,d]	Falconidae	†*Caracara seymouri*	*Caracara*
			†*Milvago brodkorbi*	*Milvago*
			Falco sparverius	*F. sparverius*
			Falco femoralis	*F. femoralis*
			Falco peregrinus	*F. peregrinus*
	Psittaciformes[a,d]	Psittacidae	*Forpus coelestis*	*F. coelestis*
	Passeriformes[e]	Thamnophilidae	*Thamnophilus bernardi*	*T. bernardi*
		Melanopareiidae	*Melanopareia elegans*	*Melanopareia elegans*
		Tyrannidae	*Myiozetetes similis*	*M. similis*
			Myiodynastes bairdii	*M. bairdii*
		Hirundinidae	*Progne* sp.	*Progne*
			Tachycineta stolzmanni	*T. stolzmanni*
			Petrochelidon rufocollaris	*P. rufocollaris*
			Hirundo rustica	*H. rustica*
		Mimidae	*Mimus longicaudatus*	*M. longicaudatus*
		Thraupidae	*Piezorina cinerea*	*P. cinerea*
			Sicalis sp.	*Sicalis*
			Sicalis taczanowskii	*S. taczanowskii*
			Sporophila peruviana	*S. peruviana*
		Emberizidae	*Rhynchospiza stolzmanni*	*R. stolzmanni*
		Icteridae	*Amblycercus holosericeus*	*A. holosericeus*
			†*Icterus icterus*	*Icterus*
			Icterus mesomelas	*I. mesomelas*
			Dives warszewiczi	*D. warszewiczi*
			†*Euphagus magnirostris*	*Euphagus*
			Molothrus bonariensis	*M. bonariensis*
			†*Molothrus* sp. nov.	*Molothrus*
			Leistes bellicosus	*L. bellicosus*

The overlap between distributions was determined using the QGIS 3.16 software (QGIS Development Team, 2021). The climatic variables *mean annual temperature* (bio01, MAT), *max temperature of warmest mon*th (bio05, MTWM*), min temperature of coldest month* (bio06, MTCM), and *annual precipitation* (bio12, AP) were extracted from the overlapping area using RStudio Team (2020) and then compared against their current values in the Talara region obtained from the nearest meteorological station "La Esperanza" (https://www.senamhi.gob.pe, Servicio Nacional de Metereología e Hidrología del Perú). La Esperanza is 53 km south of the Talara locality, about 6 m above sea level, and both sites are located in the Hyperdesertic North Peruvian Province (Rivas-Martínez et al., 2011) with similar current climate values (Zevallos and Lavado-Casimiro, 2022).

4. Results and discussion

4.1. Mutual Ecogeograhic Range by vertebrate groups

The overlap area representing the optimal modern climatic conditions for NLR communities is different for each of the vertebrate groups (Figs. 3–4). The birds present the largest overlap area, which includes the Oregonian, Californian, Baja Californian, Mohavian, Sonoran, Austroriparian, Texan, and Tamaulipan provinces in North America; the Mexican transition zone; and much of Central and South America (Escalante et al., 2021; Escalante and Morrone, 2020). The mammals present a more restricted overlap area, comprising the Guajira, Magdalena, Cauca, and Western Ecuador provinces in northwestern South America (Escalante and Morrone, 2020). The reptiles have the smallest overlap area, comprising Magdalena, Cauca, and Western Ecuador provinces in northwestern South America (Escalante and Morrone, 2020). The overlap area using mammals and reptiles together includes just the Cauca and Western Ecuador provinces (Escalante and Morrone, 2020) and the overlap area using all groups together includes only the southern portion of the Cauca province (Escalante and Morrone, 2020).

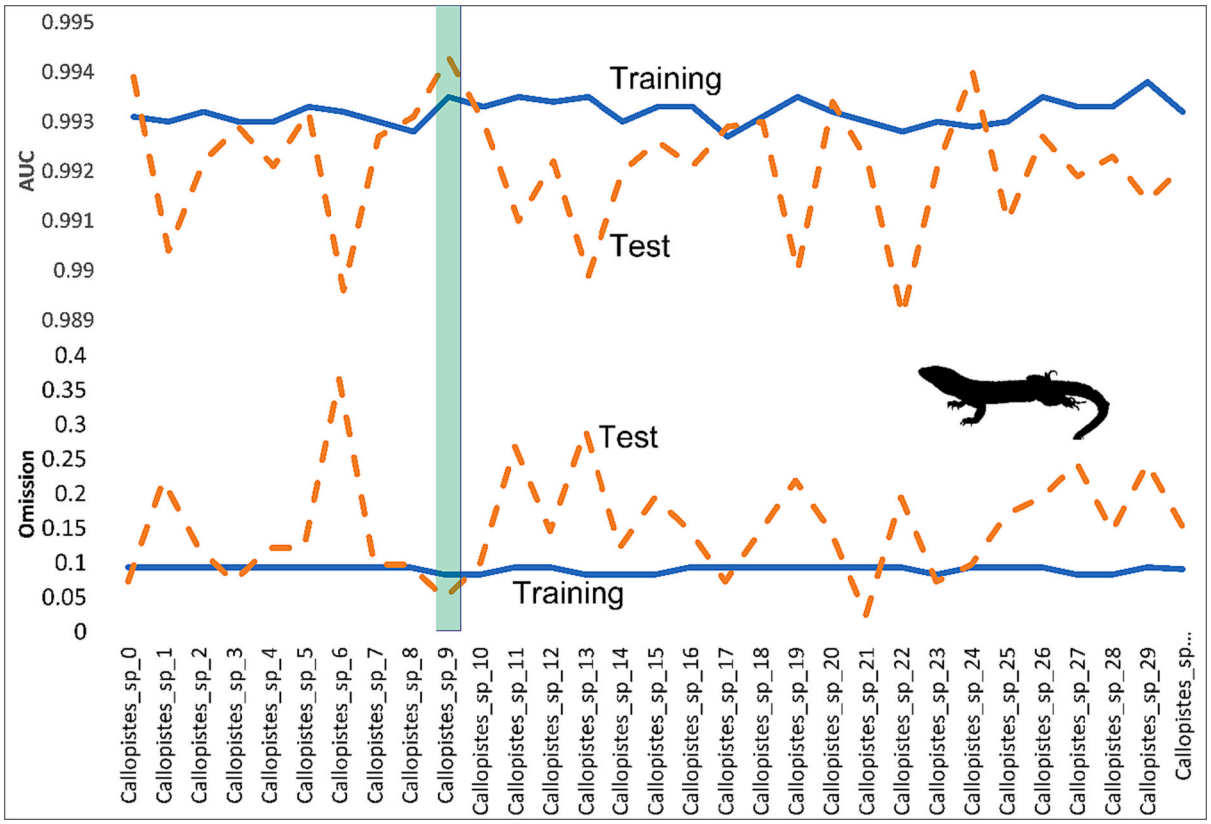

Fig. 2. Performed 30 models for each Nearest Living Relative (NLR) taxon (example shown *Callopistes* sp.) and chose the model with the highest Area Under the Curve (AUC) value and the lowest omission rate value for test (orange dashed line) and training (blue solid line) data used in the model. In the example shown *Callopistes* sp. 9 was the best model.

4.2. Paleoclimatic inferences

Individual taxa may not be reliable indicators of paleotemperature and/or paleoprecipitation on their own and in our analysis different microvertebrate groups yielded different inferences regarding the paleoclimate of the Talara region (Table 2, Fig. 5). Since the community represents a group of species that occurred together in a specific geographical location and time period, and thus were subjected to a shared set of environmental filters (Keddy and Laughlin, 2021), we view the paleoclimatic data derived from the all-groups analysis as the most reliable for paleoclimate reconstruction (Table 2). We thus use the results of the all-groups analysis as a point of comparison to evaluate the paleoclimatic inferences for each individual group of vertebrates.

The paleotemperature inference using all vertebrate groups for Late-Pleistocene Talara (~14,500–17,000 cal years BP) indicates a cooler (−1.52 °C) mean annual temperature (MAT), a cooler (−2.67 °C) max temperature of warmest month (MTWM), and slightly cooler (−0.44 °C) min temperature of coldest month (MTCM) in the Late Pleistocene versus today. The paleoprecipitation analysis indicates that Late Pleistocene Talara was significantly wetter than it is today, with an inferred annual precipitation (AP) in the Late Pleistocene versus 67.83 mm today, a difference of more than 928 mm (Table 2, Fig. 5).

This quantitative paleoclimatic reconstruction of Talara using fossil microvertebrates represents an important contribution to understanding the Quaternary of this region. To-date the only published paleoenvironment al inferences for Talara are based on qualitative analysis of sediments (Lemon and Churcher, 1961; Alván-De la Cruz et al., 2009), as well as some taxa (Churcher, 1966;Campbell, 1979, Oswald and Steadman, 2015). Quantitative paleoenvironmental information has been obtained from archaeological sites (Sandweiss, 2003), but these postdate the youngest age obtained on the Talara seeps by well over 1000 years. Quantitative information about paleoclimate in the region includes ice core oxygen isotopes records from Huascaran, Peru (Thompson et al., 1995, 2003); El Niño records in southwestern Ecuador (Rodbell et al., 1999); and fossil pollen and rat middens records from Atacama Region, Chile (Betancourt et al., 2000; Grosjean et al., 2001; González-Pinilla et al., 2021).

The paleotemperature analysis from Talara (~14,500 and 17,000 cal years BP) indicates −1.52 °C colder MAT with respect to the present (Table 2, Fig. 5), suggesting that the Late Pleistocene MAT was only slightly different from modern conditions. These results suggest that the fossil assemblage was deposited during an interstadial period, possibly the Bølling interstadial. These results are consistent with the paleotemperatures inferred by Thompson et al. (1995, 2003) from Huascaran, Peru, where Pierrehumbert (1999) using a simple Rayleigh distillation model, argued that Huascaran isotopic shift could be explained by tropical LGM temperatures only 3 °C cooler than present.

The inference of the substantially higher Pleistocene precipitation (Table 2, Fig. 5) is consistent with studies from the Atacama Desert region where between ~10,000–17,000 cal years BP the climate was much wetter (Betancourt et al., 2000; Grosjean et al., 2001; González-Pinilla et al., 2021). A significantly wetter Pleistocene climate at Talara has also been suggested based on qualitative sedimentology studies (Alván-De la Cruz et al., 2009), which inferred humid climates with regular intensity of rainfall. This wetter climate in not attributable to increased El Niño activity, which appears to have been depressed between ~15,000 to about 7000 calendar years BP (Rodbell et al., 1999).

4.3. Paleoclimatic fidelity of different vertebrate groups

All combinations of vertebrate groups separately and together infer a cooler MTWM and wetter Late Pleistocene AP with respect to the present

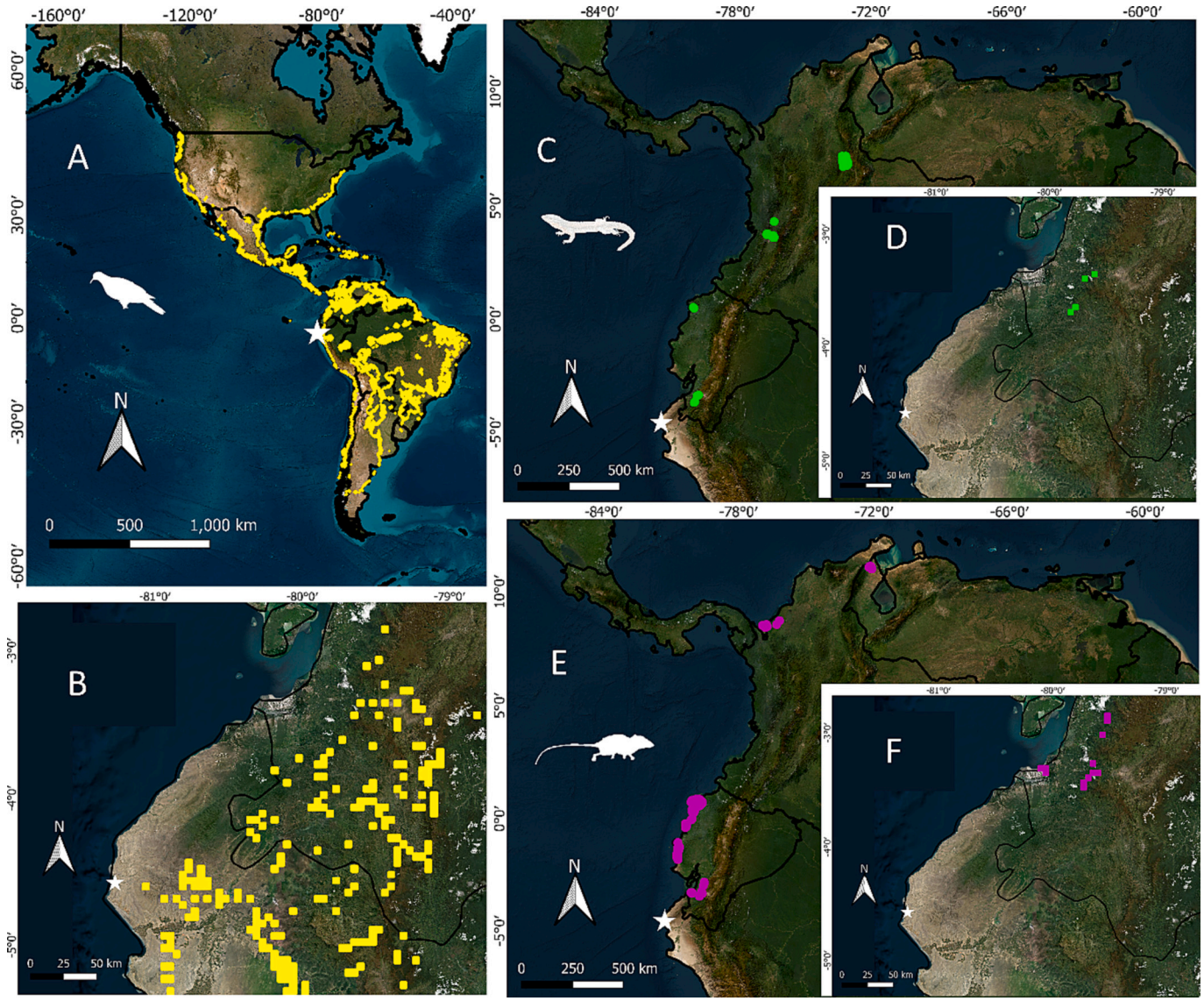

Fig. 3. Mutual Ecogeographic Range maps showing specific locations that today exhibit the optimal climatic conditions for all Nearest Living Relatives (NLR's) of small vertebrate species from Talara, including: birds (A, B), reptiles (C, D), and mammals (E, F). Figs. B, D, F are enlargements of the Talara region and demonstrate that none of the vertebrate groups infer the current climate conditions around the Talara Tar Seeps paleontological site (white star).

(Table 2, Fig. 5). Mammals are the only group that infer a warmer MAT and the highest estimated MTCM, inferring (respectively) +1.7 °C and +3.14 °C more than all-groups paleoclimatic reconstruction. In both these respects, mammals are an outlier with regard to the paleoclimate inferences obtained using the full microvertebrate community, and we thus consider them a poor group to infer Late Pleistocene MAT and MTCM in Talara tar seeps site. Birds on the other hand yield the lowest MAT and MTCM inferences with −0.48 °C and −2.45 °C, respectively, and the highest value of MTWM with +1.32 °C with respect to the all-group paleoclimatic reconstruction. We thus conclude that birds are a good group to infer MAT but a poor group to infer Late Pleistocene MTCM and MTWM in Talara. Reptiles infer slightly warmer MAT (+0.15 °C), slightly cooler MTWM (−0.59 °C), and warmer MTCM (+1.18 °C) with respect to the data obtained using all vertebrates combined, indicating that reptiles are a good proxy for MAT and MTWM, and bad proxy to infer MTCM climatic measures from the Late Pleistocene of Talara tar seeps. (Table 2, Fig. 5).

Reptiles and birds infer highest annual paleoprecipitation values (AP = +590.3 mm and + 530.6 mm, respectively), overestimating the precipitation as inferred from the all-group analysis. Mammals infer similar precipitation as the all-group analysis (AP = +89 mm), indicating that they are a good proxy for inferring paleoprecipitation while reptiles and birds are not (Table 2, Fig. 5).

Some studies (López-García et al., 2010a, 2010b, 2011a, 2011b, 2012a, 2012b, 2013, 2014a, 2014b, 2016, 2021; Bañuls-Cardona et al., 2012; Rey-Rodríguez et al., 2016; Arroyo-Cabrales et al., 2021; Cruz et al., 2021b, 2023; Piñero et al., 2024) infer paleoenvironmental conditions using mammals and herpetofauna together; therefore we also compared the paleoclimatic reconstruction obtained with all vertebrate groups against just reptiles + mammals (Table 2, Fig. 5). This combined community infers a slightly warmer MAT (+0.69 °C) and MTWM (+0.08 °C), warmer MTCM (+1.38 °C), and slightly wetter conditions (AP = +217.1 mm) with respect to all-groups paleoclimatic reconstruction. This paleoclimatic reconstruction is similar to that obtained with all vertebrates, except MTCM, eliminating the deficiencies of mammals in inferring the paleotemperature and those of reptiles for inferring the paleoprecipitation. We thus conclude that mammals + reptiles together is a good proxy for paleoclimatic reconstruction in this system.

This has also been found in studies from the Iberian Peninsula

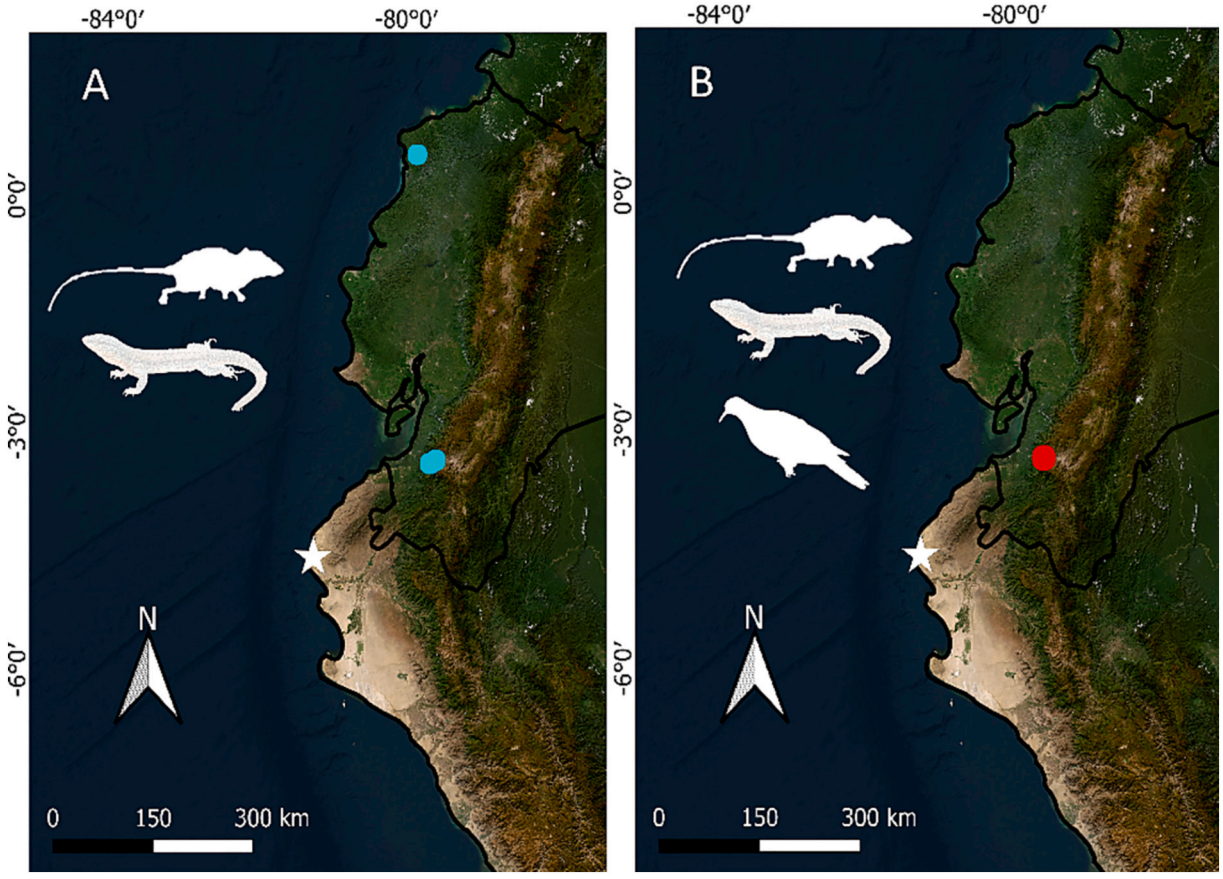

Fig. 4. Mutual Ecogeographic Range areas showing specific location that today exhibit the optimal climatic conditions for all Nearest Living Relatives (NLR's) of Talara small mammals and reptiles combined (A) and all vertebrate groups combined (B). Neither of these communities infer the current climate conditions around the paleontological site (white star).

Table 2
Late Pleistocene paleoclimatic reconstruction of Talara Tar Seeps using the Nearest Living Relatives (NLR) of all vertebrate communities (mammals + reptiles + birds) combined, compared against just mammals + reptiles combined, and against mammals, reptiles, and birds as separate groups. We showing the difference between the average of paleoclimatic reconstruction with the Present-Day climatic conditions in Talara.

	MAT	AP	MTWM	MTCM
Present-Day_Talara	**24.30** ± 2.66	**67.83** ± 132.22	**31.58** ± 1.25	**16.79** ± 1.07
Difference	0	0	0	0
All vertebrates	**22.77** ± 0.01	**996** ± 0.01	**28.91** ± 0.01	**16.35** ± 0.01
Difference	-1.52	928.18	-2.67	-0.44
Mammals and reptiles	**23.46** ± 1.32	**1213.1** ± 388.83	**28.99** ± 0.36	**17.73** ± 2.44
Difference	-0.84	1145.275	-2.59	0.94
Mammals	**24.47** ± 1.74	**1085** ± 517.94	**29.33** ± 1.35	**19.49** ± 2.44
Difference	0.18	1017.18	-2.25	2.7
Reptiles	**22.92** ± 1.47	**1586.3** ± 326.39	**28.32** ± 1.68	**17.53** ± 1.49
Difference	-1.38	1518.475	-3.26	0.74
Birds	**22.29** ± 4.63	**1526.6** ± 828.44	**30.23** ± 3.96	**13.90** ± 6.90
Difference	-2.00	1458.78	-1.35	-2.89

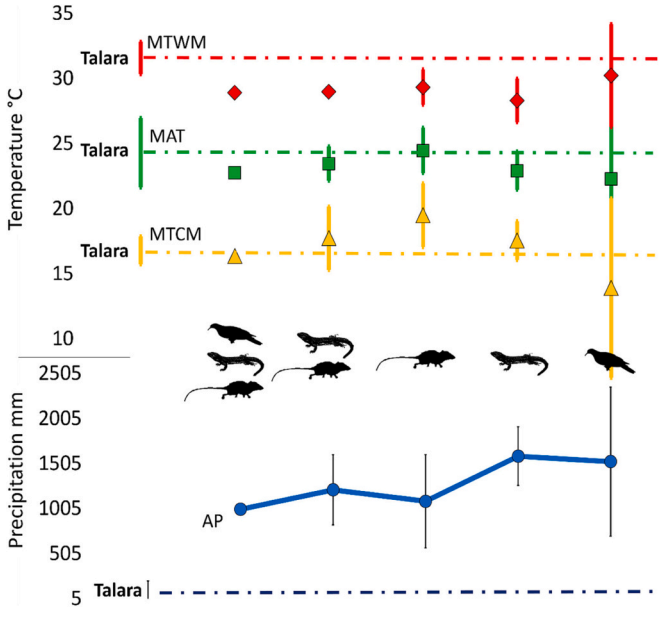

Fig. 5. Paleoclimatic reconstruction of Talara Tar Seeps site with the different groups of vertebrates including the Max Temperature of Warmest Month (MTWM, red diamonds); Mean Annual Temperature (MAT, green squares); Min Temperature of the Coldest Month (MTCM, yellow triangles), and Annual Precipitation (AP, blue circles) compared with the modern climate in Talara (dashed lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(López-García et al., 2010a, 2010b, 2011a, 2011b, 2012a, 2012b, 2013, 2014a, 2014b, 2016, 2021; Bañuls-Cardona et al., 2012; Rey-Rodríguez et al., 2016), México (Arroyo-Cabrales et al., 2021; Cruz et al., 2023), and Argentina (Cruz et al., 2021b). In all these cases the paleoclimatic reconstructions based on mammals + reptiles agreed with other proxies such as pollen, isotopes, diatoms, and sediments.

Reptiles are a good indicator of paleotemperature because they depend on external heat sources to regulate their body temperature. Thus, climate is a key factor influencing the distribution and abundance of herpetofaunal species (Brattstrom, 1956; Vitt and Caldwell, 2014; Böhm et al., 2016; Diele-Viegas et al., 2020). The poor predictivity of mammals for paleotemperature is likely due to endothermy, making adult mammals more resilient to temperature fluctuations (Nord and Giroud, 2020). Climate change has been shown to not be the causal mechanism underlaying changes in phenology, body weight or litter size in small mammals (Boutin and Lane, 2014).

Paleoprecipitation reconstruction using vertebrates is historically challenging and subject to large uncertainties (Porch, 2010; Blain et al., 2018). In this study, reptiles were a poor proxy to infer precipitation at Late Pleistocene Talara; however, other studies have inferred that the richness of Paleartic reptiles is hightly correlated with precipitation (Böhm et al., 2016). Therefore, is necessary to carry out more studies about the relationship between reptiles and precipitation in the Neotropics.

Pleistocene birds have previously been used in quantitative (Nuñez-Lahuerta et al., 2018, 2021, 2022; Arroyo-Cabrales et al., 2021; Cruz et al., 2023) and qualitative (Steadman et al., 2015; Steadman and Franklin, 2017) paleoenvironmental reconstructions in the Neotropics. Birds can provide valuable paleoclimate information (Nuñez-Lahuerta et al., 2018), as they are affected by the summer temperature and precipitation (Pearce-Higgins et al., 2015), and birds are good proxies to inferred habitat changes in Quaternary sites (Nuñez-Lahuerta et al., 2021, 2022). However, they are not a good indicator of MTWM and MTCM, and their high vagility and phenotypic plasticity make birds a problematic proxy since they can respond rapidly to environmental changes (Jonzén et al., 2006; Charmantier et al., 2008; Youngflesh et al., 2021; McLean et al., 2022). Therefore, paleoenvironmental analyses with birds must be carefully taken (Nuñez-Lahuerta et al., 2021, 2022).

5. Conclusions

Our analysis of the fossil vertebrate community from the Talara tar seeps yields an inference of mean annual temperature = 22.77 °C and annual precipitation = 996 mm in the Late Pleistocene (~14,500–17,000 cal years BP). This inferred paleoclimate is slightly cooler (−1.52 °C) and significantly wetter (+928.18 mm) than the present, which could explain how the region, now a coastal desert, was able to support high megafaunal biomass and species diversity during the Pleistocene. The fossil assemblage at Talara may represent a community during the Bølling interstadial, wich is consistent with preliminary radiocarbon dates obtained on fossils from the site.

Each group of vertebrates (reptiles, mammals, and birds) yields different climatic information; the best paleoclimatic reconstructions resulted from combining all vertebrate communities (mammals + birds + reptiles), but mammals + reptiles combined yielded inferences nearly as good as the all-groups analysis. Individually, birds were a poor paleoclimatic proxy, mammals were a good proxy to infer paleoprecipitation, and reptiles were a good proxy to infer paleotemperatures.

This study represents only the second time that biogeographical and climatic niche information of vertebrates has been used for paleoclimatic reconstruction in South America (Cruz et al., 2021a). This technique has been applied for paleoenvironmental reconstructions in other parts of the world such as Europe (Polly and Eronen, 2011; Blain et al., 2018; Villa et al., 2018a, 2018b), and North America (Smith and Polly, 2013; Cruz et al., 2016, 2021a, 2021b, 2023; Medina-Castañeda et al., 2022). It is also the second time that this method has been used with birds (Cruz et al., 2023). The use of climatic niche and biogeographical information of fossil vertebrates can be used to infer paleoclimatic conditions if other types of proxies (e.g. pollen, diatoms, glacial records, isotopes) are not available.

The paleoclimatic inference with vertebrates in this work offer an opportunity to understand the desertification process in Talara (Guevara, 1999): based on this study, we know that during the Late Pleistocene (~14,500–17,000 cal years BP) the climate was significantly wetter than the present. Subsequent studies could help identify the moment where desertification begins, and elucidate the causes of this ecosystem state shift.

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Author contribution

JAC and ELL conceived of the project, writing, review and editing the manuscript, JAC performed the formal analysis and data curation, ELL validated the data and raised the funds.

CRediT authorship contribution statement

J. Alberto Cruz: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Emily L. Lindsey:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data for the mutual ecogeographical range is available at https://zenodo.org/uploads/10257955

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