UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
BIOLOGÍA EVOLUTIVA

Influencia de la variación climática como límite biogeográfico en linajes simpátricos de *Leptotila verreauxi* (Aves: Columbidae) en el Istmo de Tehuantepec, México.

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

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QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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Ciudad Universitaria, CD. MX   **septiembre 2023**

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OFICIO FCIE/DAIP/337/2023

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e.

Me permito informar a usted que en la reunión del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **22 de mayo de 2023** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Biología Evolutiva** del (la) alumno(a) **ESPINOSA CHÁVEZ ORLANDO JAEL** con número de cuenta **310143587** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Highly divergent sympatric lineages of *Leptotila verreauxi* (Aves: Columbiadae) sugget a secondary contact area in the Isthmus of Tehuantepec, Mexico",** que es producto del proyecto realizado en la maestría que lleva por título **"Influencia de la variación climática como límite biogeográfico en linajes simpátricos de *Leptotila verreauxi* (Aves: Columbidae) en el Istmo de Tehuantepec, México"** ambos realizados bajo la dirección del **DR. LUIS ANTONIO SÁNCHEZ GONZÁLEZ**, quedando integrado de la siguiente manera:

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

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 01 de agosto de 2023

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

c. c. p. Expediente del alumno

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RESUMEN

Debido a su compleja historia geográfica y a la presencia de marcadas diferencias ambientales, el Istmo de Tehuantepec (IT) es reconocido por promover la divergencia de numerosos taxa de tierras bajas y altas. La Paloma Arroyera (*Leptotila verreauxi*), es una especie politípica ampliamente distribuida en las tierras bajas del continente americano. Presenta cuatro subespecies distribuidas en México, tres de las cuales convergen en el IT, formando una zona de contacto. La información molecular indica que las poblaciones en contacto divergieron hace aproximadamente 2,5 millones de años y que presentan una alta diferenciación genética. Además, dos de estos linajes coexisten en los bosques secos ubicados al sur del IT. En este estudio, utilicé modelos correlativos de nicho ecológico (ENM) para comparar los nichos ecológicos de cada uno de los linajes (pruebas de identidad y similitud de nicho), e identificar mediante pruebas de *blob* y *ribbon-rangebreak*, si las diferencias ambientales representan límites biogeográficos relevantes para el origen y mantenimiento de la divergencia. Modelé proyecciones de nicho ecológico al pasado durante el Holoceno Medio, el Último Máximo Glacial y el Último Interglaciar para identificar cambios en las áreas de idoneidad ambiental a través de los periodos mencionados y su posible efecto sobre las poblaciones. Mis resultados sugieren que los factores climáticos/ecológicos pueden explicar la diferenciación y la formación de una zona de contacto secundario en el IT. Las comparaciones de nicho ecológico indicaron que los nichos de los linajes simpátricos en el IT no son idénticos, pero sí son similares. Por otra parte, las pruebas de *rangebreak* mostraron que no hay barreras biogeográficas asociadas a la diferencia marcada de condiciones ambientales entre bosques tropicales secos y húmedos, sin embargo, sí indicaron la presencia de regiones con menor idoneidad en las zonas de contacto entre poblaciones divergentes. Estos resultados sugieren que la diferenciación genética pudo originarse por un evento vicariante, probablemente relacionado con factores ambientales que favorecieron la diferenciación de nichos. La ausencia de barreras biogeográficas físicas, pero la presencia de zonas ambientalmente menos idóneas en las regiones de contacto, sugieren que las zonas de contacto secundario también pueden ser mantenidas por factores climáticos para el grupo este del IT, pero también por interacciones bióticas para el grupo oeste del IT. Los resultados obtenidos aportan un panorama de los posibles procesos ecológicos que han contribuido al origen y mantenimiento de la divergencia en las poblaciones de *Leptotila verreauxi* que están en contacto en el IT.

Palabras clave: Filogeografía, límite biogeográfico, contacto secundario, Modelos de Nicho Ecológico, bosques tropicales húmedos y secos.

ABSTRACT

Due to its complex geographic history and environmental differences, the Isthmus of Tehuantepec (IT) is known to promote the divergence of numerous lowland and highland taxa. The White-tipped Dove (*Leptotila verreauxi*) is a polytypic species widely distributed in the lowlands of the American continent. It has four subspecies recognized in Mexico, three of which converge in the IT, forming a contact zone. Molecular information suggests that the populations in contact diverged approximately 2.5 million years ago and that they have high levels of genetic differentiation. Furthermore, two of these lineages coexist in the dry forests south of the IT. In this study, I used correlative ecological niche models (ENMs) to compare the ecological niches of each of the lineages (tests of niche identity and similarity) and identify, using *blob* and *ribbon-rangebreak* tests, whether environmental differences represent biogeographic boundaries relevant to the origin and maintenance of divergence in the White-tipped Dove. I modeled ecological niche projections into the past during the Middle Holocene, Last Glacial Maximum, and Last Interglacial to identify changes in areas of environmental suitability across the periods just mentioned, as well as their possible effect on populations. My results suggest that climatic and ecological factors may explain the differentiation, as well as in the formation of a secondary contact zone in the IT. Ecological niche comparisons indicated that the niches of sympatric lineages in the IT are not identical but are similar. On the other hand, environmental niche models across the region did not indicate the existence of biogeographic barriers associated with marked difference in environmental conditions between dry and humid tropical forests but did indicate the presence of regions with lower fitness in contact zones between divergent populations. These results suggest that genetic differentiation may have originated from a vicariant event, probably related to environmental factors that favored niche differentiation. The absence of a biogeographic barrier, but the presence of environmentally less suitable zones in the contact regions, suggest that secondary contact zones may also be maintained by climatic factors for the eastern IT group, but also by biotic interactions for the western IT group. The results obtained provide an overview of possible ecological processes that have contributed to the origin and maintenance of divergence in *Leptotila verreauxi* populations that are in contact in the IT.

Keywords: Phylogeography, biogeographic limit, secondary contact, Ecological Niche Models, humid and dry forests.

INTRODUCCIÓN GENERAL

El Istmo de Tehuantepec (IT) es reconocido desde hace tiempo como uno de los accidentes geográficos más influyentes en la diversificación de un gran número de taxa en la región norte de Mesoamérica. Se ubica en el sureste de México, en la porción oriental de los estados de Oaxaca y Veracruz incluyendo parte de Tabasco y Chiapas (Barrier *et al*, 1998), corresponde a una región con una compleja historia geológica (Ferrusquia-Villafrance, 1993) y paleoclimática (Mayewski *et al*., 2004; Shackleton, 2000; Wogau *et al*., 2019). Se conforma por dos vertientes: una al norte, ubicada junto a las aguas del Golfo de México, y otra al sur, junto a las aguas del Pacífico. Ambas unidas por un valle con una elevación promedio de 250m (Barber y Klicka, 2010; Barrier *et al*., 1998; Binford, 1989). El Istmo representa la zona más estrecha de México, lo que permite el contacto entre los bosques tropicales húmedos de las tierras bajas de la vertiente del Golfo y los bosques tropicales secos de tierras bajas que predominan en la vertiente del Pacífico (Ferrusquia-Villafrance, 1993).

El gradiente entre bosques tropicales secos y húmedos se define como una barrera ecológica que podría limitar el flujo de genes entre poblaciones en un eje norte-sur, promoviendo la diferenciación fenotípica de las poblaciones de tierras bajas. Esto lleva, en algunas especies, al reconocimiento de subespecies asociadas a cada hábitat (*e.g*, Binford, 1989). Sin embargo, algunas especies de aves muestran un patrón de diferenciación este-oeste (*e. g*., Sánchez-González *et al*., 2022). Por tanto, podemos asumir que la historia geográfica y ecológica del IT ha generado patrones y procesos biogeográficos complejos en la región (Binford, 1989; Castillo-Chora *et al*., 2021; Friedmann *et al*., 1950; Hogan, 1999; Llanes-Quevedo *et al*., 2022; L. A. Sánchez-González *et al*., 2022).

Algunos estudios sobre aves de tierras altas distribuidas en bosques templados al este y oeste del IT han resaltado su papel crucial como barrera biogeográfica (Barber y Klicka, 2010; Ornelas *et al*., 2013; Tsai *et al*., 2019; Venkatraman *et al*., 2019). En un estudio realizado por Barber y Klicka (2010) con 10 especies de aves que habitan en el IT, se detectó que algunas poblaciones

divergieron a causa de dos eventos discretos: uno relacionado con los cambios en el hábitat impulsados por el clima, y otro debido a una posible vía marítima formada durante el Plioceno tardío. Por otra parte, Ornelas *et al.* (2013) analizaron la divergencia temporal y espacial de 15 especies en la región, incluyendo plantas, roedores y aves, sugiriendo que las rupturas filogeográficas correspondientes al IT son consistentes con un modelo vicariante causado por múltiples mecanismos operando en distintos momentos. Sin embargo, el papel del IT en la diversificación de aves de tierras bajas ha sido poco estudiado (*e. g.*, Sosa-López *et al.*, 2013). Esto se debe probablemente a que las especies de tierras bajas no presentan barreras geográficas evidentes y, aparentemente, pueden dispersarse libremente por toda la región (Binford, 1989; Edwards y Lea, 1955), lo que impide una divergencia completa en estos taxa.

Además de los procesos históricos, es importante considerar el papel de los procesos ecológicos en la interpretación de los patrones biogeográficos (Warren *et al.*, 2014). Por lo tanto, resulta interesante explorar si el gradiente ecológico presente en el IT tiene un papel relevante en la divergencia de los linajes, actuando como límite biogeográfico. También, es fundamental identificar el papel de las fluctuaciones climáticas del Pleistoceno en la estructura actual de las poblaciones. El Pleistoceno es un periodo en el que se generó gran parte de la biodiversidad que conocemos actualmente, o un periodo en el que la biodiversidad originada en periodos anteriores tuvo que responder a condiciones dramáticamente cambiantes (Peterson y Ammann, 2013).

Durante el Pleistoceno, se produjeron una serie de cambios climáticos entre periodos fríos (glaciares) y cálidos (interglaciares) (Dansgaard *et al.*, 1993). Estos cambios alternados probablemente influyeron en la diversificación y distribución de las especies durante el último millón de años (Peterson, 2012) promoviendo modificaciones en la distribución de algunas de ellas, que lograron persistir gracias a poblaciones refugio en áreas específicas con condiciones climáticas favorables (*e.g*, Castillo-Chora *et al.*, 2021).

En este estudio, abordé los patrones de diferenciación en Istmo de Tehuantepec utilizando como modelo de estudio a la Paloma Arroyera (*Leptotila*

verreauxi). La Paloma Arroyera es una especie politípica de amplia distribución que se encuentra principalmente en tierras bajas tropicales, desde el extremo sur de Estados Unidos (el Valle Inferior del Río Grande en el sur de Texas) hasta el norte de Argentina (Friedmann *et al*., 1950). La diferenciación fenotípica entre subespecies es leve y se diagnostican principalmente con base en la coloración del plumaje. Actualmente se reconocen 13 subespecies (Gill *et al*., 2021), cuatro de las cuales se distribuyen en México: *L. v. angelica,* se distribuye en gran parte de México, su rango va desde el sur de Texas en la vertiente del Golfo, y el sur de Sonora y Chihuahua en la vertiente del Pacífico hasta el noroeste de Chiapas; *L. v. capitalis*, endémica de las islas Tres Marías, Sinaloa, es muy similar a *L. v. angelica* pero ligeramente más grande; *L. v. fulviventris*, residente del sureste de México incluyendo la península de Yucatán, su distribución al sur de la península ocupa parte de la vertiente del Atlántico en Belice y Guatemala; y *L. v. bangsi*, desde la región del Soconusco en la costa de Chiapas (Friedmann *et al*., 1950) hasta Honduras y el oeste de Nicaragua en la vertiente del pacífico (Gill *et al*., 2021; Hogan, 1999).

Fenotípicamente, la subespecie *L. v. angelica* se caracteriza por tener plumas rémiges con margen rufo estrecho, coloración blanca en el área ventral posterior (crissum y vent), los costados del pecho y la nuca de color verde cobrizo, frente grisácea, coronilla blanquecina y la punta blanca de las plumas rectrices es ancha. El resto de subespecies mexicanas son similares a *L. v. angelica*; la subespecie *L. v. capitalis* se diferencia por ser ligeramente más grande, *L. v. fulviventris* tiene un tono fuertemente amarillento o "buffy" en la parte ventral posterior (menos blanquecina), tono marrón en el dorso y nuca de color vináceo metálico (menos verde); y *L. v. bangsi* tiene el margen rufo de las rémiges más amplio y el vientre de un tono más amarillento (Giese, *et al*., 2020).

Las áreas de distribución de las tres subespecies continentales mexicanas de *L. verreauxi* colindan en el IT (Friedmann *et al*., 1950), lo que sugiere una historia biogeográfica compleja en la región. Se espera que: a) la diferenciación genética corresponda con la estructura ecológica, donde la diferenciación principal ocurriría en un eje norte-sur a través del gradiente ambiental; b) la diferenciación en el nicho

ecológico sea consistente con los tratamientos taxonómicos actuales; y c) las zonas de contacto se mantengan en función de diferencias ambientales locales.

El nicho ecológico se puede definir como el hipervolumen n-dimensional dentro del cual se encuentran las condiciones bióticas y abióticas adecuadas para la supervivencia y persistencia de una especie (Hutchinson, 1957). Basándonos en la idea anterior, podemos estimar el nicho ecológico de las especies en función de las condiciones ambientales óptimas para su supervivencia. Utilicé modelos correlativos de nicho ecológico (MNE) para estimar las áreas de idoneidad ambiental de cada uno de los tres linajes a partir de puntos de ocurrencia y un conjunto de variables ambientales (Phillips *et al.*, 2017). Además, modelé proyecciones al pasado durante el Holoceno Medio y el Pleistoceno tardío (Último Máximo Glaciar y Último Interglaciar). También probé hipótesis de conservadurismo de nicho y evalué el papel de las diferencias ambientales en la región del Istmo de Tehuantepec como límite biogeográfico.

Para las proyecciones al pasado, utilicé el paquete de R "*Grinnell*", que permite estimar el área de accesibilidad histórica o "M" a partir de simulaciones considerando procesos de dispersión, colonización e información de cambio en las condiciones climáticas a través del tiempo usando las capas ambientales del Último Máximo Glaciar (Machado-Stredel *et al.*, 2021). También utilicé el paquete "*KUENM*" (Cobos *et al.*, 2019), diseñado para robustecer el proceso de calibración y creación de los MNE, elaborando un conjunto de modelos candidatos con el fin de seleccionar los más óptimos a partir de ciertos parámetros.

Para probar las hipótesis de conservadurismo de nicho y evaluar el papel de límites biogeográficos asociados a las diferencias ecológicas, utilicé el paquete "*ENMTools*" (Warren *et al.*, 2021), que emplea MNE y métodos estadísticos para proporcionar una gran variedad de herramientas como pruebas de identidad/similitud para observar las diferencias en los nichos ecológicos, así como las pruebas de *blob* y *ribbon-rangebreak* para evaluar el papel de barreras ambientales en la distribución de las especies (Glor y Warren, 2011).

Con el fin de formular y probar hipótesis filogeográficas en la región, es crucial integrar datos históricos y ecológicos en un marco geográficamente explicito

(Mastretta-Yanes *et al*., 2015; Peterson y Ammann, 2013; Warren *et al*., 2014). Este estudio tiene como objetivo analizar el papel del gradiente ecológico en el Istmo de Tehuantepec como posible límite biogeográfico y cómo los cambios climáticos del Pleistoceno pueden haber influido en la distribución y diferenciación de las poblaciones simpátricas de *L. verreauxi*. Se sugiere la intervención de eventos vicariantes relacionados a cambios en las condiciones ecológicas lo cual ha sido previamente descrito en diferentes grupos bióticos, como en aves, mamíferos y reptiles (*e.g.* Whitmore and Stewart, 1965, Arcangeli *et al*., 2018; Butler *et al*., 2023; Gray *et al*., 2019; Ornelas *et al*., 2013; Parkinson *et al*., 2000; Zarza *et al*., 2008).

Highly divergent sympatric lineages of *Leptotila verreauxi* (Aves: Columbidae) suggest a secondary contact area in the Isthmus of Tehuantepec, Mexico

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Abstract

Due to a complex geological and biotic history, the Isthmus of Tehuantepec (IT), has been long recognized as a driver for the evolutionary divergence of numerous lowland and highland taxa. Widely distributed in the lowlands of the American continent, the White-Tipped Dove (*Leptotila verreauxi*) is a polytypic species with 13 recognized subspecies. Four of these have been recorded in Mexico, and the distribution of three abuts at the IT, suggesting a contact zone. To estimate phylogenetic patterns, divergence times and genetic differentiation, we examined two mtDNA (ND2 and COI) and one nDNA (β-fibint 7) markers. We also used correlative ecological niche models (ENM) to assess whether ecological differences across the IT may have acted as a biogeographical boundary. We estimated paleodistributions during the Middle Holocene, Last Glacial Maximum and Last Interglacial, to evaluate the influence of climate changes on the distribution and demographic changes. Our results showed genetically distinct lineages that diverged approximately 2.5 million years ago. Climatic and ecological factors may have played a dual role in promoting differentiation, but also in the formation of a secondary contact zone in the southern IT. Our ecological niche comparisons indicated that the ecological niche of sympatric lineages at the IT are not identical, but are similar; in addition, environmental niche models across the region indicated no abrupt biogeographic barriers, but the presence of regions with low suitability. These results suggest that genetic differentiation originated by a vicariant event probably related to environmental factors favoring the evolution of different ecological niches. Also, the absence of a biogeographic barrier but the presence of less suitable areas in the contact regions, suggest that secondary contact zones may be also maintained by climatic factors for the eastern group, but also by biotic interactions for the western group.
Keywords: Phylogeography, biogeographical boundary, secondary contact, Isthmus of Tehuantepec, humid and dry forests.

1 Introduction

Mesoamerica is characterized by a complex geological history, a rugged topography (see Ferrusquia-Villafranca, 1993), and complex paleoclimatic dynamics (Shackleton, 2000; Wogau et al., 2019). These traits have been highlighted as major drivers that have shaped the biotic evolutionary history in the region (Morrone, 2010; Ornelas et al., 2013; Stull, 2023). Some of the most important effects of geological and climatic dynamics on Mesoamerican biota are in range shifts in the species distribution, demographic history changes, and genetic divergence, all of which has motivated the increase of phylogeographic studies throughout the region (García-Moreno et al., 2004; Navarro-Sigüenza et al., 2008; Vázquez-Miranda et al., 2009; Ortiz-Ramírez et al., 2016; Rodríguez-Correa et al., 2017)

Located in southeastern Mexico, the Isthmus of Tehuantepec (IT) has been long recognized as one of the most important geographic features in the diversification of a large number of taxa in northern Mesoamerica (Binford, 1989; Peterson et al., 1999; Barber and Klicka, 2010; Ornelas et al., 2013). Studies in montane-forest birds distributed east and west of the IT have suggested its crucial role as a geographic barrier acting in different times or "pulses" (Barber and Klicka, 2010; Ornelas et al., 2013; Tsai et al., 2019). However, the role that IT has played in the diversification of lowland birds is still poorly understood (see Sosa-López et al., 2013), probably because it has been long assumed that lowland bird species can disperse freely throughout the region (Edwards and Lea, 1955; Binford, 1989), thus preventing complete divergence in these taxa (e.g., Howell and Webb, 1995).

The IT represents the narrowest zone in Mesoamerica, allowing contact between the dry tropical lowland forests of the Pacific slope, and the humid tropical lowland forests of the Gulf slope. This gradient has been defined as an ecological barrier that may have limited gene flow between populations in a north to south axis, promoting phenotypic differentiation of lowland populations, and even leading to the recognition of subspecies in each habitat (Binford, 1989). In addition, a few lowland species show an east-west differentiation pattern

(e.g., Sánchez-González et al. 2023). Therefore, the geographical and ecological history of the IT suggest complex biogeographical patterns and processes in the region (Friedmann et al., 1950; Binford, 1989; Hogan, 1999; Castillo-Chora et al., 2021; Llanes-Quevedo et al., 2022; Sánchez-González et al., 2022).

The White-tipped Dove (*Leptotila verreauxi*) is a widely distributed polytypic species mainly distributed in tropical lowlands from extreme southern USA (the Lower Rio Grande Valley in southern Texas) through Mexico and Central America to northern Argentina (Friedmann et al., 1950). Currently, 13 subspecies are recognized (Gill et al., 2021), four of which are distributed in Mexico: *capitalis*, endemic to the Tres Marias Islands; *angelica*, from southern Texas in the Gulf slope, and southern Sonora in the Pacific slope south to the IT; *fulviventris*, from the IT on the Gulf slope to the Yucatan Peninsula, and *bangsi*, from the Soconusco region in coastal Chiapas (Friedmann et al., 1950) to Honduras and western Nicaragua (Hogan, 1999; Gill et al., 2021). The ranges of the three Mexican mainland *L. verreauxi* subspecies abut at the IT (Friedmann et al., 1950), suggesting a complex biogeographic history in the region. As currently described, the main differentiation occurs in a west-east axis (*angelica – bangsi, fulviventris*). Such west to east differentiation, apparently follows a geographic pattern opposite to what may be expected given the environmental gradient.

Here, we approached genetic differentiation patterns at IT using *L. verreauxi* as a model. Given that the distribution of three subspecies abut at the region, we expected that: a) genetic differentiation corresponds to the ecological structure, in which main differentiation would occur in a north to south axis across the environmental gradient, b) ecological niche differentiation, which would support current taxonomic treatments, and c) contact zones maintained by local environmental differences. We performed phylogenetic and population genetics analyses using two mitochondrial and one nuclear marker, and estimated divergence times between lineages to explore genetic variation and historical

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population dynamics, focusing particularly on the on the populations at the IT. In addition, we used correlative ecological niche models (ENM) to estimate paleodistributions of lineages and test hypotheses of niche conservatism, as well as evaluate the role of ecological differences as a biogeographic limit in these populations. All of these tests allowed us to establish if these distribution patterns may be the result of secondary contact, which would suggest a vicariant event at the IT, as has been previously suggested for several taxa in different biotic groups (Parkinson et al., 2000; Zarza et al., 2008; Ornelas et al., 2013; Arcangeli et al., 2018; Gray et al., 2019; Butler et al., 2023), and to evaluate if there are differences in the ecological niche that could be contributing to the maintenance of differentiation.

2 Materials and methods

2.1 Taxon sampling

We obtained 38 tissue samples from the collection of the Museum of Zoology "Alfonso L. Herrera" (MZFC), representing all Mexican subspecies (Table S1). We supplemented our samples with sequences available in GenBank (Benson et al., 2013; www.ncbi.nlm.nih.gov; Table S1). Outgroups were selected based on a previous phylogenetic hypothesis (Johnson and Weckstein, 2011) and included six species: *L. jamaicensis*, *L. cassini, L. megalura, L. rufaxilla*, *L. plumbeiceps* and *Leptotrygon veraguensis*. In total we included 68 individual genetic sequences, considering samples deposited in GenBank.

2.2 Laboratory protocols

DNA was extracted using both a Qiagen DNeasy Blood and Tissue Kit following the manufacturer's protocol, as well as a phenol-chloroform extraction protocol (Sambrook and Russell, 2006). We amplified and sequenced two mitochondrial DNA markers (NADH, dehydrogenase subunit 2 [ND2] and the cytochrome C oxidase subunit 1 [COI]); and one

nuclear marker (the *β-fibrinogen intron 7* [β-fibint 7]) via the polymerase chain reaction (PCR) following standardized protocols (Lorenz, 2012). We used primers L5215-H5766 and 487L-H6313 (Sorenson et al., 1999) for ND2, L6626-H7005 (Hafner et al., 1994) for COI, and B17L-B17U (Prychitko and Moore, 1997) for β-fibint 7. These molecular markers have shown high efficiency when analyzing phylogenetic relationships and biogeographic patterns in Columbiformes, in addition to show high phylogenetic consistency between mtDNA and nDNA in some studies at the supraspecific level (Johnson and Clayton, 2000; Pereira et al., 2007; Johnson and Weckstein, 2011; Sweet and Johnson, 2015; Sweet et al., 2017; Sangster et al., 2018). PCR products were visualized in agarose gels (1.3%) stained with ethidium bromide (0.5 µl/ml). Purification and sequencing processes were performed at Macrogen Inc., South Korea. Chromatograms were edited using Geneious Prime 2019.0.4 (Kearse et al., 2012) and multiple alignments were performed using MAFFT (Katoh and Standley, 2013) with default parameters.

2.3 Model selection and phylogenetic analyses

Partition schemes and sequence evolution models for Bayesian Inference were selected using PartitionFinder v2.1.1 (Lanfear et al., 2017). Molecular evolution models selected for each of the partition schemes are shown in Table S2. Phylogenies were generated using Maximum Likelihood (ML) and Bayesian Inference (BI). For ML, we used RAxMLGUI (Silvestro and Michalak, 2012), with the selected partition scheme, the GTR substitution model and the algorithm "ML + rapid bootstrap" (Stamatakis et al., 2008), and 10,000 iterations. We used MrBayes for estimating BI trees, which were obtained using the partition schemes and selected models as previously described (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). We ran 10,000,000 generations in four parallel runs and eight Markov Chain Monte Carlo (MCMC) sampling every 1,000 generations. We

used Tracer 1.7 (Rambaut et al., 2018) to determine a stationary phase and the burn-in, and used FigTree v1.4.3 (Rambaut, 2009) to visualize the consensus tree.

2.4 Divergence time estimation

Divergence times were estimated in BEAST v.1.10.4 (Suchard et al., 2018) using the partition schemes and substitution models previously selected. We applied a strict molecular clock with a Yule speciation process (Steel and McKenzie, 2001). Since we were analyzing genetic patterns at intraspecific level, we opted for a strict molecular clock, which assumes a single rate of constant evolution throughout the phylogeny (Pybus, 2006). We applied a substitution rate of 1.96% for the mitochondrial markers (Sweet and Johnson, 2015; Sweet et al., 2017), and a substitution rate of 0.53% for β-fibint 7 (Johnson and Clayton, 2000). Two independent runs of 20,000,000 generations were generated starting from different random points, corroborating the –lnL values and values of the effective sample sizes (ESSs) >200 for all of the parameters in Tracer 1.7 (Rambaut et al., 2018). We used LogCombiner for combining the output files and TreeAnnotator (Drummond A., 2015) for obtaining a maximum credibility tree (MCCT) with a burn-in of 25% and a posterior probability limit of 0.5%.

2.5 Genetic variation and historical demography

As a measure of genetic differentiation between populations, we calculated genetic fixation from the F_{ST} estimator, and interpreted its values based on Hartl et al., (1997). From this index, the rate of gene flow between populations or *Nm* can be estimated, the higher this value the higher the gene flow (Nei, 1987). Genetic distances were measured using the Nei corrected distance parameter D_{xy} (Nei, 1987). Populations were identified according to the phylogeny and haplotype networks. Historical demography analyses were calculated for each clade via *mismatch* distributions, and their significance was assessed using the

raggedness index *I* (Rozas et al., 2017). All phylogeographic tests and genetic diversity estimates were obtained in DnaSP v.6.12.01 (Rozas et al., 2017). Given that ND2 and COI have different sample size numbers, we built different haplotype networks in Network 10.1 using a Median Joining Network algorithm (Bandelt et al., 1999). We assessed genetic variation in *L. verreauxi* via an Analysis of Molecular Variance (AMOVA) in Arlequin 3.5.2.2 (Excoffier et al., 2005). Significance was estimated via two independent analyses with 16,000 permutations based on pairwise differences: one included all populations, while another included only populations present in the IT, to test whether the levels of variation were consistent when only these populations are considered.

2.6 Ecological niche models

Since Pleistocene climatic changes have significantly influenced the evolution and bigeography of lowland taxa in the IT (Castillo-Chora et al., 2021, Sánchez-González et al., 2023), we estimated paleodistribution models for populations of *L. verreauxi* during the Middle Holocene (MH, ~6000 years ago), Last Glacial Maximum (LGM, ~21,000 years ago), and Last Interglacial (LIG, ~120,000 - 140,000 years ago), as well as for the Present. For model building, we used the data corresponding to occurrence records of *L. verreauxi* that we used in molecular analyses, supplemented with those downloaded from the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.f7wwag). Duplicated and erroneously georeferenced records were filtered and eliminated for analyses, and we performed a randomized spatial thinning with the R package "spThin" (Aiello-Lammens et al., 2015), which allowed us to build highly accurate models by reducing biases associated to data concentration in some geographic areas. Based on the genetic structure, we divided the total data into three datasets corresponding to each lineage present in the IT. Given that geographic boundaries for each lineage in this lowland taxon are not clear, we generated polygons from occurrence data corresponding to unequivocally assigned genetic samples;

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this procedure allowed us to reduce identification bias for records from biological collections identified below the species level (Fig. S3).

We downloaded environmental variables for the present and for past scenarios corresponding to the MH, LGM, and LIG from WorldClim 1.4 (Hijmans et al., 2005) with a resolution of 2.5 minutes. For the MH and the LGM models, we used layers from three different Atmosphere-Ocean General Circulation Models: CCSM4 (Community Climate System Model) (Gent et al., 2011), MIROC-ESM (Model for Interdisciplinary Research On Climate) (Hasumi and Emori, 2004), and MPI-ESM-P (Max Planck Institute) (Baehr et al., 2015); layers corresponding to the present and the LIG were downloaded from the CCSM4 model. We retained environmental variables with a greater contribution to the present distribution ranges, while variables with high collinearity were eliminated via the variance inflation factor (VIF), with a VIF<10 as implemented in the R package "corrplot" (Wei and Simko, 2021). We therefore selected nine bioclimatic variables: mean diurnal range (BIO2), isothermality (BIO3), max temperature of warmest month (BIO5), mean temperature of wettest quarter (BIO8), precipitation of wettest month (BIO13), precipitation of driest month (BIO14), precipitation seasonality (BIO15), precipitation of warmest quarter (BIO18) and precipitation of coldest quarter (BIO19).

We used the "Grinnell" v.0.0.21 R package (Machado-Stredel et al., 2021) to define an accessibility area (M) for each lineage (Fig. S2) based on estimates of the historical accessible area derived from simulations considering biological processes such as dispersal, colonization, and information on climate change over time. These M areas were further refined through comparisons with the terrestrial ecoregions (Dinerstein et al., 2017), and biogeographic provinces of the Neotropics layers (Morrone, 2014). All environmental models corresponding to the present and projections to the past were generated using the maximum entropy algorithm in Maxent v3.4.4 (Phillips et al., 2017) as implemented in "KUENM" v 1.1.9 package (Cobos et al., 2019), that is designed to strengthen the model

calibration and creation process, via the generation of a set of candidate models to select one or several optimal models from certain parameterizations. Finally, to explore potential regions with low reliability for model transference to the past, we performed extrapolation risk analyses via the Mobility-oriented parity (MOP) test in "NicheToolbox" (Osorio-Olvera et al., 2020). The final models were edited in QGIS v3.18 (QGIS Development Team, 2022; http://www.qgis.org/).

2.7 Niche conservatism and *range-breaking tests*

Due to the absence of conspicuous geographic barriers across the lowland distributional range of *L. verreauxi*, we explored if genetic structure has been maintained through ecological niche differentiation in the different lineages detected in Mesoamerica. We compared the ecological niches through paired tests of niche conservatism between each lineage; additionally, we tested whether environmental differences across the IT may act as an ecological barrier separating these lineages. All these analyses were performed using "ENMTools" (Warren et al., 2021).

Niche conservatism models were generated in Maxent v.3.4.4 (Phillips et al., 2017) to perform pairwise comparisons between the observed lineages. These analyses compare the overlapping of empirical models with a null distribution constructed from a set of pseudo-replicates using Monte Carlo methods. Empirical and pseudoreplicated values were calculated for all tests from measures of niche overlap (Schoener's *I* and *D*) via 100 replicates to generate the null distribution across all tests. We also tested whether niches differ from what is expected by chance via a niche equivalence test (or identity test) and the symmetric background similarity test (Warren et al., 2021). To assess the role of environmental differences as a barrier for dispersal of the lineages across the IT, we used blob and ribbon range-breaking tests (Glor and Warren, 2011). Blob range-breaking test evaluates whether regions occupied by each lineage are more environmentally different than

expected by chance; if so, the environmental differences would represent an abrupt biogeographical barrier. On the other hand, ribbon range-breaking test assesses whether unsuitable habitat divides areas of suitable habitat for each of the lineages which may function as a biogeographical boundary (Warren et al., 2021). We selected two areas that may functioning as a barrier for dispersal (the "ribbon") in this lowland taxon: 1) the Sierra del Tolistoque, in the southern IT, and 2) the wetland region in the southern Gulf of Mexico (Fig. 1). These two areas may serve as barriers due to apparent environmental differences on each side, maintaining lineage divergence despite confirmed overlap between the NA and NCA lineages in the southern IT. To optimize the ribbon range-breaking test, we generated a set of random points within the two selected areas due to the small number of occurrence records.

3 Results

We obtained 48 sequences corresponding to ND2 (1041 base pairs, bp), 26 to COI (379 bp) and 16 to β-fibint 7 sequences (1136 bp). mtDNA topologies obtained from IB and ML analyses were highly similar. The tree showed two highly supported monophyletic groups for *L. verreauxi* (Fig. 2a), separated by the IT. One group included the North American (NA) clade, distributed west of the IT, and a few from northwestern Chiapas (geographically east of the IT); the other main group, distributed east of the IT, is subdivided in two groups, each of which present further well-supported groupings. Samples from the Soconusco region in the Pacific slope in southeastern Mexico were grouped in a Northern Central American Clade (NCA), which is sister to the Yucatán Peninsula clade (YUC), while samples from Southern Central America and northern South America (SCA) formed a clade sister to west and central South America samples (SA).

Our mtDNA phylogeographic analyses showed two sympatric lineages in the southern IT region (Fig. 1). The NA lineage is distributed across the region in both slopes,

while the NCA lineage is apparently restricted to the dry forests south of the IT. These results do not support the current taxonomic scheme for *L. verreauxi* in Mesoamerica.

The nDNA tree (Supplementary material, Fig. S1) did not showed a clear geographic structure. Most of the samples of *Leptotila* species used as outgroup were included in a group sister to several *L. verreauxi* samples. The other group included most of samples distributed west of the IT (*angelica* and *capitalis*), two samples from NCA (*bangsi*), and an outgroup species, *L. jamaicensis*. These groups shared indels that coincide in position and length, with low nodal support (PP > 0.76 and BS > 70).

3.1 Divergence times

Our data suggest an old divergence event during the Late Pliocene – Lower Pleistocene transition at approximately 2.5 Mya ago (1.94-3.43 Mya ago, 95% Height Posterior Density [HPD]) between the group west of the IT (the NA clade) and the group east of the IT. Further divergence events in the group east of the IT occurred between the clades SCA-SA and the clades NCA and YUC during the Lower Pleistocene around 1.89 Mya ago (1.39-2.49 Mya, HPD 95%). The most recent divergences occurred between NCA and Yucatan at 0.9 Mya ago (0.62-1.34 Mya HPD 95%) and between SCA and SA at 0.92-1.78 Mya, HDP 95%). A recent differentiation event between populations of the Tres Marías islands (*L. v. capitalis*) and rest of NA clade occurred around 100 kya (0.04-0.18 Ma, HDP 95%), though an apparent founder event.

3.2 Genetic structure

The haplotype network for both mDNA markers showed the same organization as in the phylogeographic tree (Fig. 2a). We found 25 haplotypes in ND2 and 8 haplotypes in COI. In both haplotype networks, we found a relatively large number of mutational steps separating two main clades roughly divided at the IT (25 in ND2 and 11 in COI), while NCA

and Yucatán clades are separated by a smaller number of mutational steps (14 in ND2 and 5 in COI). A clear star-like pattern in the NA clade suggests a sudden demographic expansion; demographic patterns in the other clades are unclear. Mismatch distributions (Fig. 2b) showed a tendency towards population expansion, although with non-significant raggedness (r) values (> 0.05) in all populations.

The F_{ST}, Nm, and D_{XY} indices showed a strong differentiation in most of the populations (Table 1). All the F_{ST} values are near to 1.0, indicating high genetic fixation, and a nearly complete haplotypic separation in all lineages, as expected in genetically structured populations. Nm in the other hand, indicated less than one migrant every four generations. Genetic distances, as measured by the Nei corrected distance parameter D_{XY} revealed high levels of genetic differentiation (> 2%) for all paired comparisons, except for NCA-YUC with 0.00748 (0.7%).

D_{XY} / F_{ST} (Nm)	NA	NCA	YUC
NA	-	0.03840	0.03659
NCA	0.97807 (0.01)	-	0.00748
YUC	0.97006 (0.01)	0.95563 (0.01)	-

Table 1. F_{ST} values (below the diagonal) and D_{XY} values (above the diagonal) for the L. verreauxi lineages. Values in the parentheses represent the number of migrants (Nm) per generation.

The AMOVA analysis (Table 2) including all populations, showed that 95.9%of the genetic variation is found between populations, while 4.06% is found within populations is, suggesting a strong population structure. The AMOVA analysis including the NA-NCA lineages, increased to 96.6% the variation between populations.

Populations	Source of variation	d.f.	Sum of squares	Variance components	Percentage variation	F_{ST}	P
All populations	Among populations	4	577.492	18.09475 Va	95.94		
	Within populations	50	38.326	0.76652 Vb	4.06	0.95936	0.0001
NA-NCA	Among populations	1	230.745	17.76667 Va	96.60		
	Within populations	40	24.993	0.62482 Vb	3.40	0.96603	0.0001

Table 2. Results of AMOVA of the L. verreauxi populations.

3.3 Distributions and paleodistributions

Distribution models for the Present and projections to the past yielded a good performance in each lineage (Table 3). For the NA clade, environmental variables with highest contribution were precipitation seasonality and precipitation of wettest month (BIO 15 = 28.1%, BIO 13 = 22.3%, respectively); while for NCA were isothermality and mean diurnal range (BIO 3 = 48.3%, BIO 2 = 30.4%, respectively). In the case of YUC, precipitation of wettest month and precipitation of warmest quarter (BIO 13 = 48.4%, BIO 18 = 8.9%, respectively).

Lineage	Regularization multiplier	Feacture classes	AUC ratio	Partial ROC	AICc	Omission rate	Parameters
NA	0.25	qp	1.4773	0	21022.95	0.05	35
NCA	3	q	1.5733	0	5963.72	0.03	7
YUC	0.5	lq	1.2037	0	4721.84	0.04	15

Table 3. Summary of model performance statistics per lineage

The areas of high environmental suitability for the three Mesoamerican lineages showed clear geographic changes in comparison to Present (Fig. 3). During the LIG, NCA and YUC showed a smaller geographic distribution in small and isolated habitat patches.

NA showed an increase in the geographic extension of the environmental suitability in southeastern Mexico and northern Central America. In LGM, NA experienced a reduction in suitable areas, being restricted to three main lowland areas in both slopes and an almost complete disappearance of suitability areas south of the IT. Regions such as YUC exhibited a decrease in environmental suitability, while NCA lineage showed an increase of the suitable conditions towards the MH. It is important to observe that all the three lineages experienced an increase in the environmental suitable areas; these areas have been apparently maintained towards the Present. According to environmental suitability maps, current contact zones across IT may have been formed until recently (at least since LGM), as most of suitable areas appear as allopatric through time intervals for which ecological modeling was conducted.

3.4 Ecological niche comparisons

Because results of *D* were similar and *I* tend to express greater variability, for e niche comparisons we focused on the *Schoener´s I*. The niche identity tests showed that the niches of each of the three lineages are not identical (*Schoener I* values lower than the pseudoreplicated values; $P < 0.01$; Table 4; Fig. S4). On the other hand, the background similarity tests indicated conserved niches, as no significant differences ($P > 0.05$) between the empirical and pseudoreplicated values for all paired comparisons were detected (Table 4; Fig. S4).

Lineages	Identity test p values		Similarity test p values		Blob rangebreak p values	
	D	*I*	*D*	*I*	*D*	*I*
NA-NCA	0.009	0.009	0.227	0.099	0.108	0.108
NA-YUC	0.009	0.009	0.376	0.396	0.198	0.207
YUC-NCA	0.009	0.009	0.108	0.089	0.108	0.029

Table 4. *P* values of the niche comparison tests (*Identity, Similarity and Blob-rangebreak*)

Range-breaking blob tests did not show empirical values with a significant deviation from the null hypothesis (P > 0.05; Table 4; Fig. S4), suggesting that no biogeographical barrier is associated with environmental differences across the IT ecological gradient. However, the ribbon range-breaking test for the NA and NCA lineages suggested the presence of a region with less suitable conditions for the NCA lineage in the contact zone (I value, P < 0.01 for the comparison of the NCA lineage vs. the ribbon; Table 5; Fig. S5). Similarly, the comparison between the NA and YUC lineages suggests the presence of a region of less suitable conditions for the YUC lineage (I value, P < 0.05 for YUC vs. the ribbon; Table 5; Fig. S6).

Lineages (L)	L1 vs. L2		L1 vs. Ribbon		L2 vs. Ribbon		Outside vs Ribbon	
	D	I	D	I	D	I	D	I
NA-NCA	0.227	0.247	0.089	0.079	0.009	0.009	0.009	0.009
NA-YUC	0.009	0.108	0.356	0.287	0.039	0.039	0.306	0.306

Table 5. P values of the *ribbon-rangebreak* test

4 Discussion

Our study illustrates both emergent patterns found in different taxa across the study region, as well as discrepancies between phenotypically-based and molecular-based taxonomies in *L. verreauxi*. Our phylogenetic tree (Fig. 2a) agrees with divergence events described in other studies along the Mexican Pacific slope and the Isthmus of Tehuantepec in which previously unexpected evolutionary patterns are being revealed (Arcangeli et al., 2018; Castillo-Chora et al., 2021; Sánchez-González et al., 2021; Llanes-Quevedo et al., 2022; Sánchez-González et al., 2023).   On the other hand, our phylogeny also shows that

traditional phenotypically-based taxonomy may fail at correspondence with evolutionary patterns, and could even conceal them. Some currently recognized Mesoamerican subspecies within *L. verreauxi* are grouped into one of the three recovered clades, which suggest that previously established boundaries for recognition of currently accepted subspecies may be incorrect. Although it is difficult to accurately stablish boundaries for lowland taxa, we found that the NA clade grouped currently recognized subspecies *angelica* (mainland Mesoamerican lowlands west of the IT), *capitalis* (from the Tres Marías islands) and probably some *fulviventris* in the southern Gulf Slope, while the NCA clade grouped samples of *bangsi* of the Pacific slope. The Yucatán clade grouped samples currently assigned to *L. v. fulviventris*. Thus, currently recognized subspecies do not fit into the evolutionary hypothesis derived from our phylogeographic analyses, which showed that different lineages are sympatric in the southern IT (southern Oaxaca).

Our phylogeographic tree showed further differentiation events in groups divided by the IT (Fig. 2a). In the group west of the IT, within NA clade, all individuals from Tres Marías islands (currently in subspecies *capitalis*) were grouped in a subclade. This structure is consistent with simple paraphyly, in which lineage sorting is shallow due to a small number of founders (Omland et al., 2006) which likely dispersed to the islands (180 – 40 kya), which consistent with islands emergence (McCloy et al., 1988) and with dispersal times in other bird species in the islands (Ortiz-Ramírez et al., 2018). In the group east of IT, genetic differentiation between sister clades YUC and NCA is relatively low (0.07%), also suggesting a recent divergence event. Genetic divergence between Mesoamerican lineages in *L. verreauxi* is very deep, underlying the role of the IT as a significant barrier for differentiation in lowland taxa. Values above traditional species thresholds for species recognition (Hebert et al., 2004; Seutin et al., 1995; Fuchs et al., 2021) were found between NA-NCA (3.8%) and between NA and YUC (3.6%), suggesting these groups may warrant full species status.

Our analyses also found deep differentiation in the SCA and the SA despite having a small number of samples.

Divergence of *L. verreauxi* from other *Leptotila* species probably occurred during the Late Miocene, in which climatic changes favored the development of extensive regions of dry vegetation all over North America (Singh, 1988), promoting a clear separation between dry and wet forests in the lowlands further south, in Mesoamerica (Graham and Dilcher, 1995; Cerling et al., 1997; Pound et al., 2012). These divergence events are consistent with the differentiation in other bird groups with similar habitats during the same time, such as in *Melanerpes* (Navarro-Sigüenza et al., 2017; Llanes-Quevedo et al., 2022), which differentiated in temperate-tropical forests and dry forests, respectively. Within *L. verreauxi*, lineage differentiation occurred during the Late Pliocene-Pleistocene (Fig. 2a) at about 2.6 Mya (1.9-3.4 Mya) with the split of lineages west (NA) and east of the IT (NCA-YUC, SCA-SA). This event is also consistent with climatic changes that led to vegetation changes across the region, likely severing connections between formerly continuous ecosystems and therefore, allowing persistence of suitable conditions within small patches (e.g., Castillo-Chora et al. 2021) which reduced gene flow between lowland populations (e.g., Sánchez-González et al., 2021, Sánchez-González et al., 2023). The star-like pattern of *angelica* in the haplotype network supports the biogeographic pattern described above, indicating recent population growth that may be result of the expansion of suitable conditions across the region.

Divergence date for the west and east groups is also consistent with proposed geographic processes in the region, such as formation of a seaway crossing the IT at approximately 2-3 million years ago during the late Pliocene (Barrier et al., 1998), which has been frequently invoked as the main promoter of vicariant events in the region for the differentiation in unrelated lowland taxa, such as mammals (Whitmore and Stewart, 1965), geckos (Butler et al., 2023), and montane birds (Ornelas et al., 2013). Seaway hypothesis,

however, has been challenged (Wyatt Durham et al., 1955; Mulcahy et al., 2006), and alternative hypothesis have been proposed, such as the ecological niche divergence (see Sánchez-González et al., 2023). Although the hypothesis related to a seaway across the IT may explain west-east divergence pattern, further differentiation events across the north to south ecological gradient have been described in other vertebrates, such as reptiles (Parkinson et al., 2000; Zarza et al., 2008; Gray et al., 2019; Butler et al., 2023).

Our analyses revealed a contact zone for the NA and NCA lineages south of the IT (Fig. 1), because genetically divergent individuals are syntopic in the seasonally dry forests foothills of the Pacific slope of the Sierra del Tolistoque, Oaxaca. Sympatric lineages with a deep genetic divergence, such as these in *L. verreauxi*, have been rarely reported in birds (Hogner et al., 2012; Benham and Cheviron, 2019), but also in other groups (Tominaga et al., 2009; Xiao et al., 2012).

Different causes may result in the establishment of a secondary contact zone (Benham and Cheviron, 2019). Sympatric distribution in genetically structured populations is typically interpreted as the result of formerly isolated lineages (Hogner et al., 2012; Benham and Cheviron, 2019). Pleistocene climatic fluctuations promoted the divergence of the west and east groups across the IT, which may have been restricted to allopatric stable climatic areas (Fig. 3). After the disappearance of the barrier (either geographical or ecological), populations are expected to expand to ecologically suitable areas. However, environmental differences in the landscape and biological interactions (e.g., competitive exclusion) between taxa with similar niches may slow down the recolonization process (Anderson et al., 2002), acting as a reinforcement that may help in maintaining differentiation over time.

Estimating ecological niches using intraspecific lineages or subspecies as units can represent their niche more accurately, without ignoring local adaptive responses as would occur when estimating models at the species level (Smith et al., 2019). Our

comparisons showed that ecological niche of the three lineages of *L. verreauxi* is not identical, but more similar than expected by chance given their environmental background (e.g., Escalante et al., 2021; Niwa et al., 2022). Thus, although each lineage in *L. verreauxi* is occupying different environments and climatic conditions, their ecological niches are similar, and therefore may evolve slowly (Peterson et al., 1999). The similarity in the ecological niches of the NA and NCA may explain, in part, their sympatric distribution in the southern IT. According to range-breaking tests, environmental differences across the north to south ecological gradient in the IT do not represent an abrupt environmental barrier for dispersal of the populations of *L. verreauxi* between habitats.

Our results suggest that contact zone in southern IT may have less suitable conditions for dispersal of NCA, than for NA. Thus, NCA populations are seemingly less tolerant to dry forest climatic conditions on Pacific slope of the IT, which likely prevents its dispersal further west. NA populations, however, seem to be tolerant to both humid and dry conditions, suggesting that other factors, such as the role of biological interactions at local scales (e.g., competition) between both lineages should be considered in maintaining this limited secondary contact zone. A further possibility is related to the seasonal differences in the precipitation between the dry forests of the southern IT and the mesic forests of the Soconusco region in coastal Chiapas (Binford, 1989): the seasonal increase of humidity would allow the dispersal of the mesic-adapted NCA further north to be in contact with NA in the southern IT. We suggest that this secondary contact zone, has been maintained through limited ecological suitability for NCA to the west of the IT, while to the east, divergence may have been maintained via ecological interactions or seasonal movements. We lack data on lineages north of the IT, where NA and YUC may overlap due to the absence of conspicuous barriers; a shallow genetic divergence however between these two lineages, suggests a corridor across the Usumacinta River drainage.

The Isthmus of Tehuantepec is an area long-recognized as a geographic limit for several North American bird families (Navarro-Sigüenza et al., 2014), as well as a promoter of speciation and ecological differentiation, particularly for montane bird taxa, which have different species divided by the Tehuantepec Valley (Barber and Klicka, 2010). However, its role as a barrier for lowland bird taxa is still poorly understood (see Binford, 1989). Patterns of divergence in lowland populations in the Isthmus region should be viewed with caution due to a dynamic biotic history, which due to changes in ecological conditions has likely promoted ecological niche differentiation, as suggested in several bird taxa (Castillo-Chora et al. 2021; Sánchez-González et al, 2021; Llanes-Quevedo et al., 2022; Sánchez-González et al, 2023).

5 Acknowledgments

6 References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132

Anderson, R.P., Peterson, A.T., Gómez-Laverde, M., 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98, 3–16.

Arcangeli, J., Light, J.E., Cervantes, F.A., 2018. Molecular and morphological evidence of the diversification in the gray mouse opossum, *Tlacuatzin canescens* (Didelphimorphia), with description of a new species. J. Mammal. 99, 138–158. https://doi.org/10.1093/jmammal/gyx173

Baehr, J., Fröhlich, K., Botzet, M., Domeisen, D.I.V., Kornblueh, L., Notz, D., Piontek, R., Pohlmann, H., Tietsche, S., Müller, W.A., 2015. The prediction of surface temperature in the new seasonal prediction system based on the MPI-ESM coupled climate model. Clim. Dyn. 44, 2723–2735. https://doi.org/10.1007/s00382-014-2399-7

Bandelt, H.-J., Forster, P., Rohl, A., 1999. Median-Joining Networks for Inferring Intraspecic Phylogenies. Mol. Biol. 16, 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Barber, B.R., Klicka, J., 2010. Two pulses of diversification across the Isthmus of Tehuantepec in a montane Mexican bird fauna, in: Proceedings of the Royal Society B: Biological Sciences. The Royal Society, pp. 2675–2681. https://doi.org/10.1098/rspb.2010.0343

Barrier, E., Velasquillo, L., Chavez, M., Gaulon, R., 1998. Neotectonic evolution of the Isthmus of Tehuantepec (southeastern Mexico). Tectonophysics 287, 77–96. https://doi.org/10.1016/S0040-1951(98)80062-0

Benham, P.M., Cheviron, Z.A., 2019. Divergent mitochondrial lineages arose within a large, panmictic population of the Savannah sparrow (*Passerculus sandwichensis*). Mol. Ecol. 0–3. https://doi.org/10.1111/mec.15049

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W., 2013. GenBank. Nucleic Acids Res. 41, D36-42. https://doi.org/10.1093/nar/gks1195

Binford, L.C., 1989. A distributional survey of the birds of the Mexican state of Oaxaca. American Ornithologists' Union.

Butler, B.O., Smith, L.L., Flores-Villela, O., 2023. Phylogeography and taxonomy of *Coleonyx elegans* Gray 1845 (Squamata : Eublepharidae) in Mesoamerica : The Isthmus of Tehuantepec as an environmental barrier. Mol. Phylogenet. Evol. 178, 107632. https://doi.org/10.1016/j.ympev.2022.107632

Castillo-Chora, V.D.J., Sánchez-González, L.A., Mastretta-Yanes, A., Prieto-Torres, D.A., Navarro-Sigüenza, A.G., 2021. Insights into the importance of areas of climatic

stability in the evolution and maintenance of avian diversity in the Mesoamerican dry forests. Biol. J. Linn. Soc. 1–18. https://doi.org/10.1093/biolinnean/blaa202

Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, L.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nat. Lond. 389, 153–158.

Cobos, M.E., Townsend Peterson, A., Barve, N., Osorio-Olvera, L., 2019. Kuenm: An R package for detailed development of ecological niche models using Maxent. PeerJ 2019, 1–15. https://doi.org/10.7717/peerj.6281

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.P.B., Van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience 67, 534–545. https://doi.org/10.1093/biosci/bix014

Drummond, A.J. Rambaut, A., 2015. Bayesian evolutionary analysis by sampling trees, in: Bayesian Evolutionary Analysis with BEAST. pp. 79–96.

Edwards, E.P., Lea, R.B., 1955. Birds of the Monserrate area, Chiapas, Mexico. The Condor 57, 31–54. https://doi.org/10.2307/1364696

Escalante, M.A., Horníková, M., Marková, S., Kotlík, P., 2021. Niche differentiation in a postglacial colonizer, the bank vole *Clethrionomys glareolus*. Ecol. Evol. 11, 8054–8070. https://doi.org/10.1002/ece3.7637

Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evol. Bioinforma. 1, 117693430500100. https://doi.org/10.1177/117693430500100003

Ferrusquia-Villafranca, I., 1993. Geology of Mexico: a synopsis. Biol. Divers. Mex. Orig. Distrib. 3–108.

Friedmann, H., Griscom, L. Moore, R.T., 1950. Distributional check-list of the birds of Mexico, part I. Pacific Coast. Avif, 29.

Fuchs, J., Bowie, R.C.K., Melo, M., Boano, G., Pavia, M., Fjeldså, J., 2021. Phylogeographical history of the Olive Woodpecker *Dendropicos griseocephalus*, a

species widely distributed across Africa. Ibis 163, 417–428.
https://doi.org/10.1111/ibi.12875

García-Moreno, J., Navarro-Sigüenza, A.G., Peterson, A.T., Sánchez-González, L.A., 2004. Genetic variation coincides with geographic structure in the common bush-tanager (*Chlorospingus ophthalmicus*) complex from Mexico. Mol. Phylogenet. Evol. 33, 186–196. https://doi.org/10.1016/j.ympev.2004.05.007

Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R., Lawrence, D.M., Neale, R.B., Rasch, P.J., Vertenstein, M., Worley, P.H., Yang, Z.L., Zhang, M., 2011. The community climate system model version 4. J. Clim. 24, 4973–4991. https://doi.org/10.1175/2011JCLI4083.1

Gill, F., Donsker, D., Rasmussen, P. (Eds), 2021. IOC World Bird List (v13.1). https://doi.org/10.14344/IOC.ML.13.1.

Glor, R.E., Warren, D., 2011. Testing ecological explanations for biogeographic boundaries. Evolution 65, 673–683. https://doi.org/10.1111/j.1558-5646.2010.01177.x

Graham, A., Dilcher, D., 1995. The Cenozoic record of tropical dry forest in northern Latin America and the southern United States.

Gray, L.N., Barley, A.J., Poe, S., Thomson, R.C., Nieto-Montes de Oca, A., Wang, I.J., 2019. Phylogeography of a widespread lizard complex reflects patterns of both geographic and ecological isolation. Mol. Ecol. 28, 644–657. https://doi.org/10.1111/mec.14970

Hafner, M.S., Sudman, P.D., Villablanca, F.X., Spradling, T.A., Demastes, J.W., Nadler, S.A., 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. Science 265, 1087–1090. https://doi.org/10.1126/science.8066445

Hartl, D.L., Clark, A.G., Clark, A.G., 1997. Principles of population genetics. Sinauer associates Sunderland.

Hasumi, H., Emori, S., 2004. K-1 Coupled GCM (MIROC) Description. K-1 Tech. Rep. 1 34.

Hebert, P.D.N., Stoeckle, M.Y., Zemlak, T.S., Francis, C.M., 2004. Identification of birds through DNA barcodes. PLoS Biol. 2, e312. https://doi.org/10.1371/journal.pbio.0020312

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high-resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276

Hogan, K.M., 1999. White-tipped Dove (*Leptotila verreauxi*), in: Poole, A., Gill, F. (Eds.), The Birds of North America No. 436. The Birds of North America, Inc., Philadelphia, P A.

Hogner, S., Laskemoen, T., Lifjeld, J.T., Porkert, J., Kleven, O., Albayrak, T., Kabasakal, B., Johnsen, A., 2012. Deep sympatric mitochondrial divergence without reproductive isolation in the common redstart *Phoenicurus phoenicurus*. Ecol. Evol. 2, 2974–2988. https://doi.org/10.1002/ece3.398

Howell, S.N.G., Webb, S., 1995. A Guide to the Birds of Mexico and Northern Central America, Oxford University Press. Oxford University Press.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Johnson, K.P., Clayton, D.H., 2000. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). Molecular Phylog. Mol. Phylogenet. Evol. 14, 141–151. https://doi.org/10.1006/mpev.1999.0682

Johnson, K.P., Weckstein, J.D., 2011. The Central American land bridge as an engine of diversification in New World doves. J. Biogeogr. 38, 1069–1076. https://doi.org/10.1111/j.1365-2699.2011.02501.x

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol. Biol. Evol. 30, 772–780. https://doi.org/10.1093/molbev/mst010

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2017. Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol. Biol. Evol. 34, 772–773. https://doi.org/10.1093/molbev/msw260

Llanes-Quevedo, A., Mastretta-Yanes, A., Sánchez-González, L.A., Castillo-Chora, V.J., Navarro-Sigüenza, A.G., 2022. The tangled evolutionary history of a long-debated Mesoamerican taxon: The Velazquez Woodpecker (*Melanerpes santacruzi*, Aves:

Picidae). Mol. Phylogenet. Evol. 170, 107445.
https://doi.org/10.1016/j.ympev.2022.107445

Lorenz, T.C., 2012. Polymerase Chain Reaction: Basic Protocol Plus Troubleshooting and
Optimization Strategies. J. Vis. Exp. JoVE 3998. https://doi.org/10.3791/3998

Machado-Stredel, F., Cobos, M.E., Peterson, A.T., 2021. A simulation-based method for
selecting calibration areas for ecological niche models and species distribution
models. Front. Biogeogr. 0, 0–23. https://doi.org/10.21425/f5fbg48814

McCloy, C., Ingle, J.C., Barron, J.A., 1988. Neogene stratigraphy, foraminifera, diatoms,
and depositional history of Maria Madre Island, Mexico: Evidence of early Neogene
marine conditions in the southern Gulf of California. Mar. Micropaleontol. 13, 193–
212. https://doi.org/10.1016/0377-8398(88)90003-5

Morrone, J.J., 2014. Biogeographical regionalisation of the Neotropical region. Zootaxa
3782, 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Morrone, J.J., 2010. Fundamental biogeographic patterns across the Mexican Transition
Zone: an evolutionary approach. Ecography 33, 355–361.
https://doi.org/10.1111/j.1600-0587.2010.06266.x

Mulcahy, D.G., Morrill, B.H., Mendelson III, J.R., 2006. Historical biogeography of lowland
species of toads (Bufo) across the Trans-Mexican Neovolcanic Belt and the
Isthmus of Tehuantepec. J. Biogeogr. 33, 1889–1904.

Navarro-Sigüenza, A.G., Rebón-Gallardo, M.F., Gordillo-Martínez, A., Peterson, A.T.,
Berlanga-García, H., Sánchez-González, L.A., 2014. Biodiversidad de aves en
México. Rev. Mex. Biodivers. 85, 476–495. https://doi.org/10.7550/rmb.41882

Navarro-Sigüenza, A.G., Townsend Peterson, A., Nyari, A., García-Deras, G.M., García-
Moreno, J., 2008. Phylogeography of the *Buarremon* brush-finch complex (Aves,
Emberizidae) in Mesoamerica. Mol. Phylogenet. Evol. 47, 21–35.
https://doi.org/10.1016/j.ympev.2007.11.030

Navarro-Sigüenza, A.G., Vázquez-Miranda, H., Hernández-Alonso, G., García-Trejo, E.A.,
Sánchez-González, L.A., 2017. Complex biogeographic scenarios revealed in the
diversification of the largest woodpecker radiation in the New World. Mol.
Phylogenet. Evol. 112, 53–67. https://doi.org/10.1016/j.ympev.2017.04.013

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press, New York.

Niwa, K., Tran, D.V., Nishikawa, K., 2022. Differentiated historical demography and
ecological niche forming present distribution and genetic structure in coexisting two

salamanders (Amphibia, Urodela, Hynobiidae) in a small island, Japan. PeerJ 10, e13202. https://doi.org/10.7717/PEERJ.13202

Omland, K.E., Baker, J.M., Peters, J.L., 2006. Genetic signatures of intermediate divergence: population history of Old and New World Holarctic ravens (*Corvus corax*). Mol. Ecol. 15, 795–808. https://doi.org/10.1111/j.1365-294X.2005.02827.x

Ornelas, J.F., Sosa, V., Soltis, D.E., Daza, J.M., González, C., Soltis, P.S., Gutiérrez-Rodríguez, C., de los Monteros, A.E., Castoe, T.A., Bell, C., Ruiz-Sanchez, E., 2013. Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened cloud forests of northern Mesoamerica. PLoS ONE 8, 56283. https://doi.org/10.1371/journal.pone.0056283

Ortiz-Ramírez, M.F., Andersen, M.J., Zaldívar-Riverón, A., Ornelas, J.F., Navarro-Sigüenza, A.G., 2016. Geographic isolation drives divergence of uncorrelated genetic and song variation in the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*; Aves: Turdidae). Mol. Phylogenet. Evol. 94, 74–86. https://doi.org/10.1016/j.ympev.2015.08.017

Ortiz-Ramírez, M.F., Sánchez-González, L.A., Castellanos-Morales, G., Ornelas, J.F., Navarro-Sigüenza, A.G., 2018. Concerted Pleistocene dispersal and genetic differentiation in passerine birds from the Tres Marías Archipelago, Mexico. The Auk 135, 716–732. https://doi.org/10.1642/auk-17-190.1

Osorio-Olvera, L., Lira-Noriega, A., Soberón, J., Peterson, A.T., Falconi, M., Contreras-Díaz, R.G., Martínez-Meyer, E., Barve, V., Barve, N., 2020. ntbox: An r package with graphical user interface for modelling and evaluating multidimensional ecological niches. Methods Ecol. Evol. 11, 1199–1206. https://doi.org/10.1111/2041-210X.13452

Parkinson, C.L., Zamudio, K.R., Greene, H.W., 2000. Phylogeography of the pitviper clade *Agkistrodon*: historical ecology, species status, and conservation of cantils. Mol. Ecol. 9, 411–420. https://doi.org/10.1046/J.1365-294X.2000.00854.X

Pereira, S.L., Johnson, K.P., Clayton, D.H., Baker, A.J., 2007. Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. Syst. Biol. 56, 656–672. https://doi.org/10.1080/10635150701549672

Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893. https://doi.org/10.1111/ecog.03049

Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., 2012. Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33Ma). Earth-Sci. Rev. 112, 1–22. https://doi.org/10.1016/j.earscirev.2012.02.005

Prychitko, T.M., Moore, W.S., 1997. The utility of DNA sequences of an intron from the β-Fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Mol. Phylogenet. Evol. 8, 193–204. https://doi.org/10.1006/mpev.1997.0420

Pybus, O.G., 2006. Model selection and the molecular clock. PLoS Biol. 4, 686–688. https://doi.org/10.1371/journal.pbio.0040151

QGIS Development Team, 2022. QGIS Geographic Information System.

Rambaut, A., 2009. FigTree v1.4.3. URL http://tree.bio.ed.ac.uk/software/figtree/ (accessed 4.22.23).

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. 67, 901–904. https://doi.org/10.1093/sysbio/syy032

Rodríguez-Correa, H., González-Rodríguez, A., Oyama, K., 2017. Perspectivas de la ecología molecular en un país megadiverso. Rev. Mex. Biodivers. 88, 3–13. https://doi.org/10.1016/j.rmb.2017.10.002

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rozas, J., Ferrer-Mata, A., Sánchez-Del Barrio, J.C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S.E., Sánchez-Gracia, A., 2017. DnaSP 6: DNA Sequence Polymorphism analysis of large data sets. Mol. Biol. Evol. 34, 3299–3302. https://doi.org/10.1093/molbev/msx248

Sambrook, J., Russell, D.W., 2006. Purification of nucleic acids by extraction with phenol:chloroform. CSH Protoc. 2006, pdb.prot4455. https://doi.org/10.1101/pdb.prot4455

Sánchez-González, L. A., Castillo-Chora, V. J., Arbeláez-Cortés, E., Navarro-Sigüenza, A. G., 2021. Diversification and secondary contact in the magpie-jays (*Calocitta*)

throughout the pacific lowlands of Mesoamerica. J. Zool. Syst. Evol. Res. 59, 2371–2386. https://doi.org/10.1111/jzs.12571

Sánchez-González, L.A., Cayetano, H., Prieto-Torres, D.A., Rojas-Soto, O.R., Navarro-Sigüenza, A.G., 2023. The role of ecological and geographical drivers of lineage diversification in the Squirrel cuckoo *Piaya cayana* in Mexico: a mitochondrial DNA perspective. J. Ornithol. 2022 1, 1–17. https://doi.org/10.1007/S10336-022-02008-W

Sangster, G., Sweet, A.D., Johnson, K.P., 2018. *Paraclaravis*, a new genus for the Purple-winged and Maroon-chested Ground-doves (Aves: Columbidae). Zootaxa 4461, 134. https://doi.org/10.11646/zootaxa.4461.1.10

Seutin, G., Ratcliffe, L.M., Boag, P.T., 1995. Mitochondrial DNA Homogeneity in the Phenotypically Diverse Redpoll Finch Complex (Aves: Carduelinae: *Carduelis flammea-hornemanni*). Evolution 49, 962–973. https://doi.org/10.2307/2410418

Shackleton, N.J., 2000. The 100,000-year Ice-age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. Science 289, 1897–1902.

Silvestro, D., Michalak, I., 2012. RaxmlGUI: A graphical front-end for RAxML. Org. Divers. Evol. 12, 335–337. https://doi.org/10.1007/s13127-011-0056-0

Singh, G., 1988. History of aridland vegetation and climate: A global perspective. Biol. Rev. 63, 159–195. https://doi.org/10.1111/j.1469-185X.1988.tb00629.x

Smith, A.B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.H., Warren, D., 2019. Niche estimation above and below the species level. Trends Ecol. Evol. 34, 260–273. https://doi.org/10.1016/j.tree.2018.10.012

Sorenson, M.D., Ast, J.C., Dimcheff, D.E., Yuri, T., Mindell, D.P., 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Mol. Phylogenet. Evol. 12, 105–114. https://doi.org/10.1006/mpev.1998.0602

Sosa-López, J.R., González, C., Navarro-Sigüenza, A.G., 2013. Vocal geographic variation in Mesoamerican Common Bush Tanagers (*Chlorospingus ophthalmicus*). Wilson J. Ornithol. 125, 24–33. https://doi.org/10.1676/12-051.1

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML Web Servers. Syst. Biol. 57, 758–771. https://doi.org/10.1080/10635150802429642

Steel, M., McKenzie, A., 2001. Properties of phylogenetic trees generated by Yule-type speciation models. Math. Biosci. 170, 91–112. https://doi.org/10.1016/S0025-5564(00)00061-4

Stull, G.W., 2023. Evolutionary origins of the eastern North American–Mesoamerican floristic disjunction: Current status and future prospects. Am. J. Bot. 110, e16142. https://doi.org/10.1002/ajb2.16142

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J., Rambaut, A., 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evol. 4. https://doi.org/10.1093/ve/vey016

Sweet, A.D., Johnson, K.P., 2015. Patterns of diversification in small New World ground doves are consistent with major geologic events. The Auk 132, 300–312. https://doi.org/10.1642/auk-14-193.1

Sweet, A.D., Maddox, J.D., Johnson, K.P., 2017. A complete molecular phylogeny of *Claravis* confirms its paraphyly within small New World ground-doves (Aves: Peristerinae) and implies multiple plumage state transitions. J. Avian Biol. 48, 459–464. https://doi.org/10.1111/jav.01077

Tominaga, K., Watanabe, K., Kakioka, R., Mori, S., Jeon, S.R., 2009. Two highly divergent mitochondrial DNA lineages within *Pseudogobio esocinus* populations in central Honshu, Japan. Ichthyol. Res. 56, 195–199. https://doi.org/10.1007/s10228-008-0071-0

Tsai, W.L.E., Mota-Vargas, C., Rojas-Soto, O., Bhowmik, R., Liang, E.Y., Maley, J.M., Zarza, E., McCormack, J.E., 2019. Museum genomics reveals the speciation history of *Dendrortyx* wood-partridges in the Mesoamerican highlands. Mol. Phylogenet. Evol. 136, 29–34. https://doi.org/10.1016/j.ympev.2019.03.017

Vázquez-Miranda, H., Navarro-Sigüenza, A.G., Omland, K.E., 2009. Phylogeography of the Rufous-naped Wren (*Campylorhynchus rufinucha*): speciation and hybridization in Mesoamerica. The Auk 126, 765–778. https://doi.org/10.1525/auk.2009.07048

Warren, D.L., Matzke, N.J., Cardillo, M., Baumgartner, J.B., Beaumont, L.J., Turelli, M., Glor, R.E., Huron, N.A., Simões, M., Iglesias, T.L., Piquet, J.C., Dinnage, R., 2021. ENMTools 1.0: an R package for comparative ecological biogeography. Ecography 44, 504–511. https://doi.org/10.1111/ecog.05485

Wei, T., Simko, V., 2021. R package "corrplot": Visualization of a correlation matrix.

Whitmore, F.C., Stewart, R.H., 1965. Miocene mammals and Central American seaways. Science 148, 180–185. https://doi.org/10.1126/science.148.3667.180

Wogau, K.H., Arz, H.W., Böhnel, H.N., Nowaczyk, N.R., Park, J., 2019. High resolution
    paleoclimate and paleoenvironmental reconstruction in the northern Mesoamerican
    frontier for prehistory to historical times. Quat. Sci. Rev. 226, 106001.
    https://doi.org/10.1016/j.quascirev.2019.106001

Wyatt Durham, J., Arellano, A.R.V., Peck, J.H., JR., 1955. Evidence for no Cenozoic
    Isthmus of Tehuantepec seaways. GSA Bull. 66, 977–992.
    https://doi.org/10.1130/0016-7606(1955)66[977:EFNCIO]2.0.CO;2

Xiao, J.H., Wang, N.X., Murphy, R.W., Cook, J., Jia, L.Y., Huang, D.W., 2012. *Wolbachia*
    infection and dramatic intraspecific mitochondrial DNA divergence in a fig wasp.
    Evolution 66, 1907–1916. https://doi.org/10.1111/j.1558-5646.2011.01561.x

Zarza, E., Reynoso, V.H., Emerson, B.C., 2008. Diversification in the northern neotropics:
    mitochondrial and nuclear DNA phylogeography of the iguana *Ctenosaura
    pectinata* and related species. Mol. Ecol. 17, 3259–3275.
    https://doi.org/10.1111/j.1365-294X.2008.03826.x

7 Figure legends

Figure 1. Geographical representation of the samples used in this study. Inset shows the
distribution of the haplogroups and the number of individuals in each area in the Isthmus of
Tehuantepec (IT). To the south is the contact zone between NA and NCA, while to the
northeast the putative contact zone along the Usumacinta River drainage.

Figure 2. a) Haplotype network and mtDNA phylogeny of *L. verreauxi*. Divergence times in
Mya. Numbers above the nodes correspond to the Bootstrap value (ML) / posterior
probability (IB); numbers below indicate 95% HPD (High Posterior Density) ranges. Black
dots in the haplotype network represent mutational steps, while open circles indicate
possible extinct or unsampled haplotypes. The dotted black box highlights the individuals
from theTres Marías Islands; the red labels in the phylogeny depict sympatric samples
from the Sierra del Tolistoque. b) Mismatch distributions, the graphs show a fit of the
empirical data with a recent population growth model for the three lineages.

Figure 3. Ecological niche models of each lineage during the present time, Middle Holocene, Last Glacial Maximum and Last Interglacial, the dark areas in the maps of the current correspond to areas of climatic stability.

Figure 1
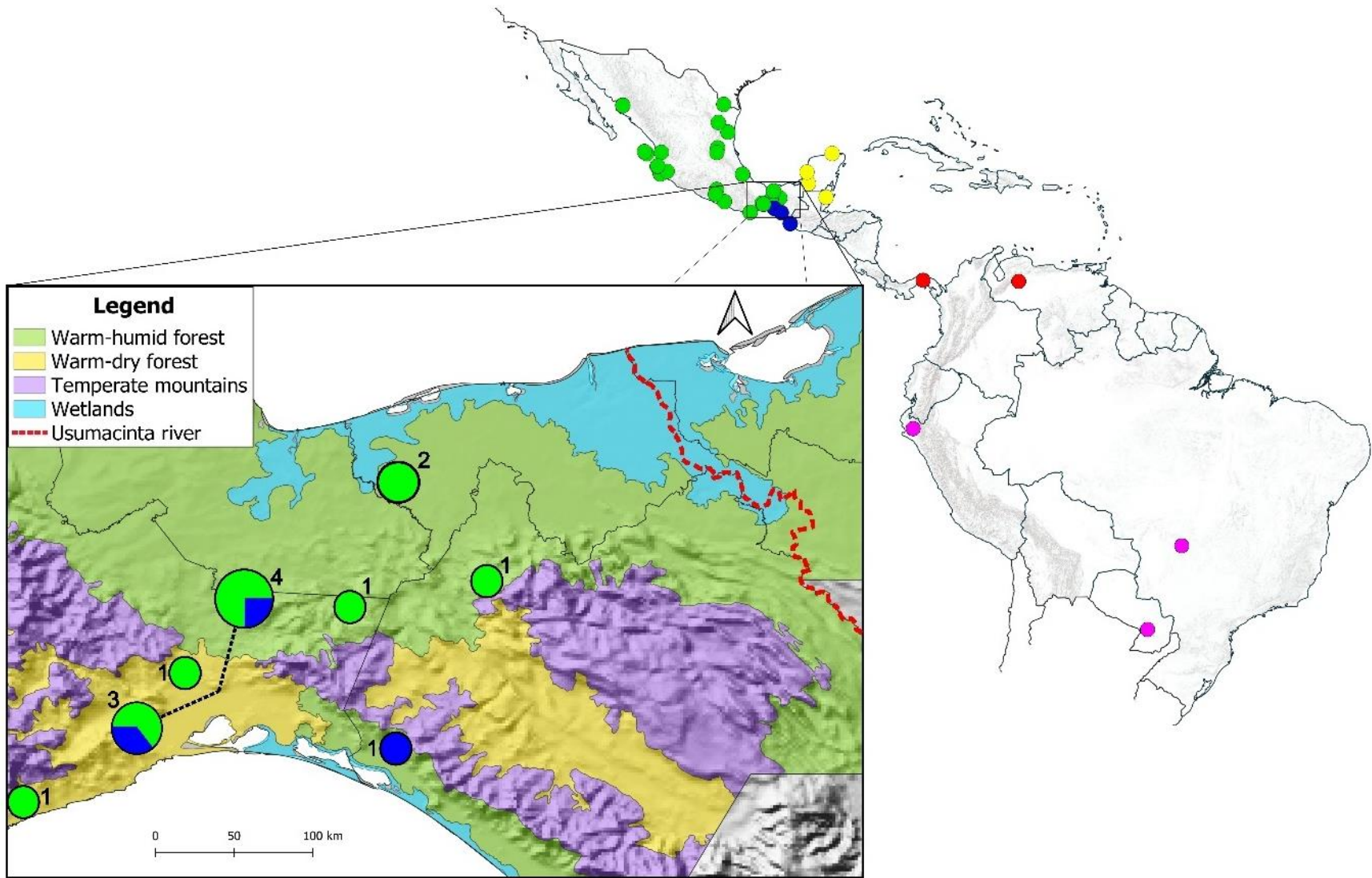
Figure 2
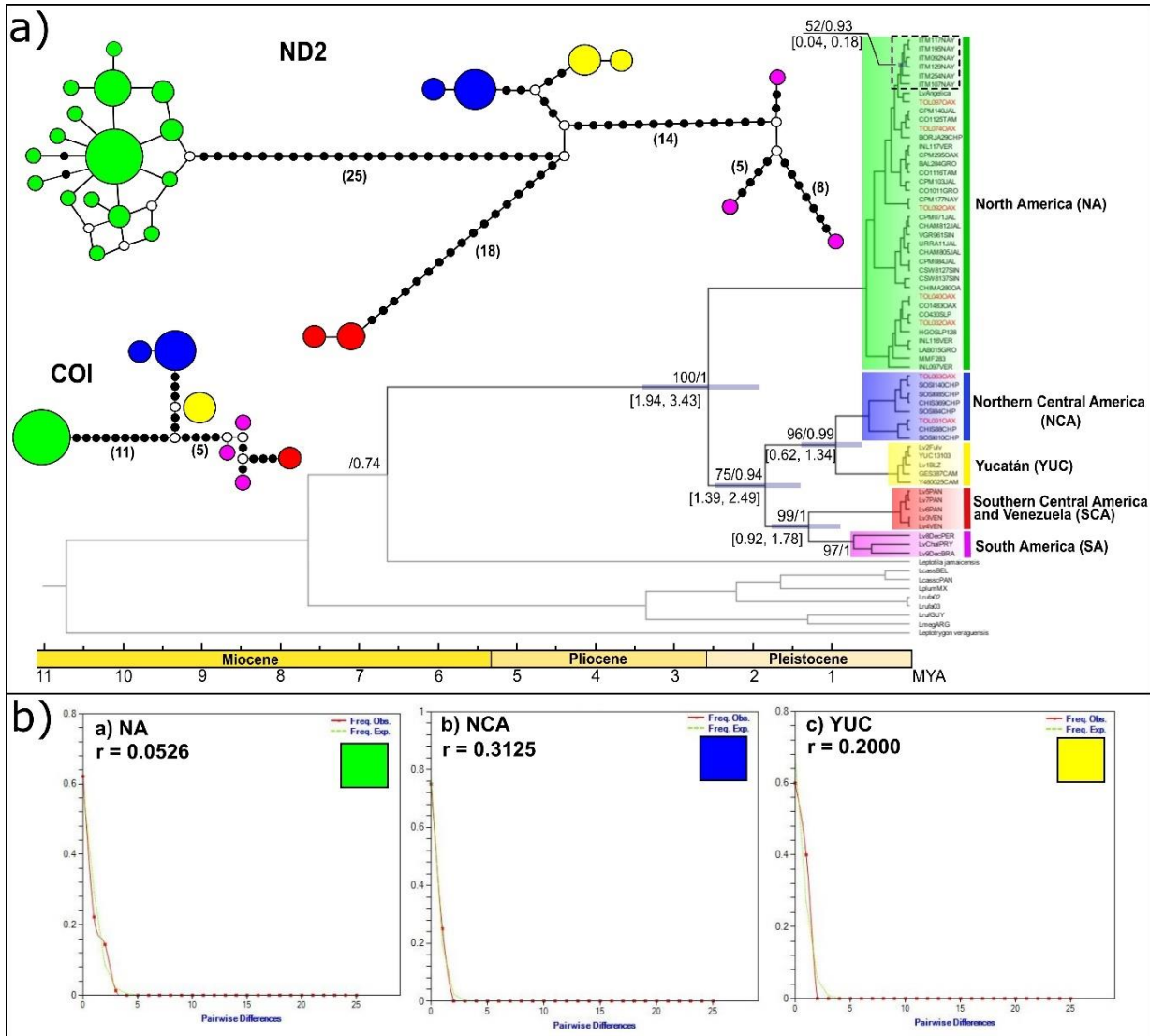
Figure 3
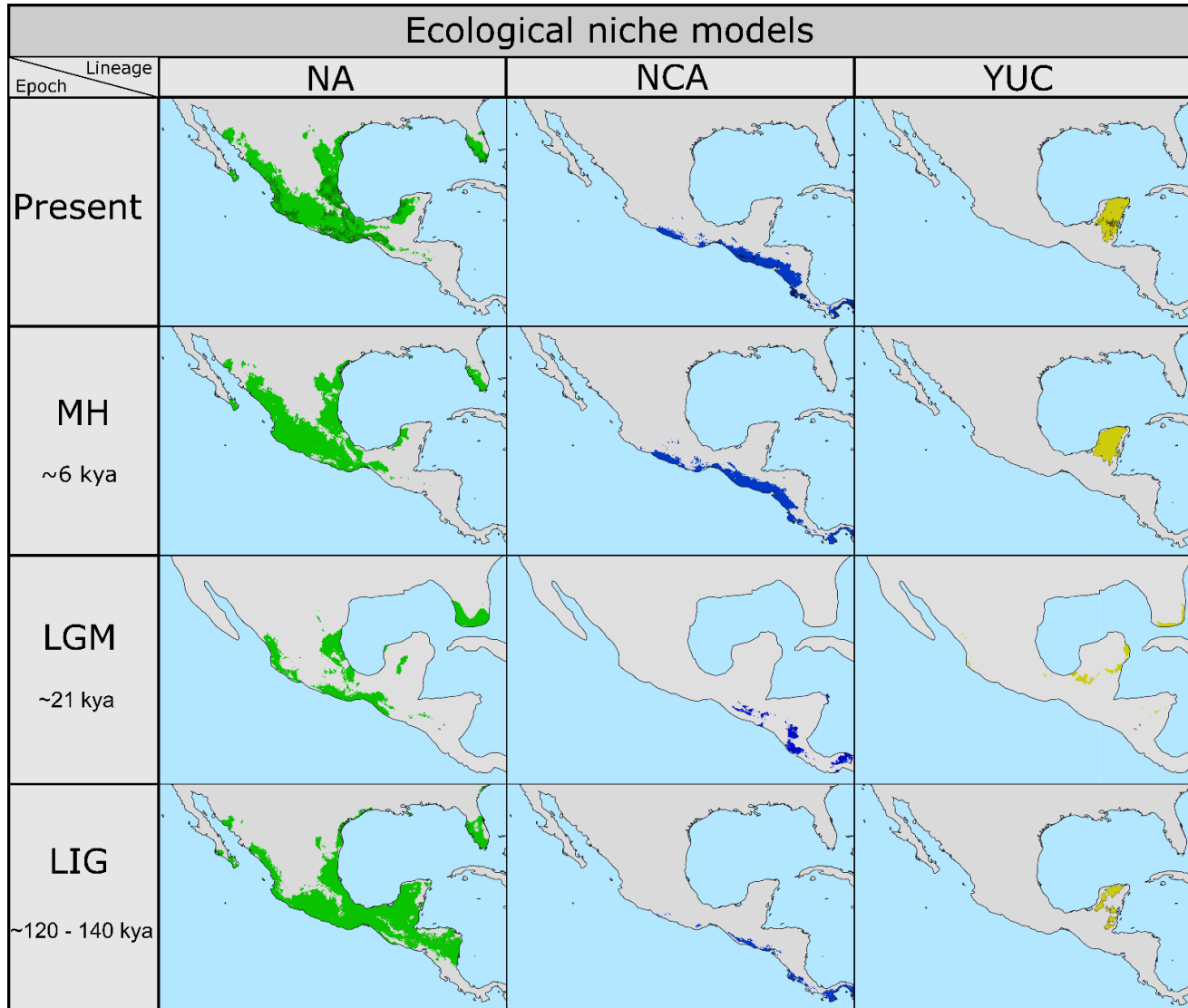
8 Supplementary materials
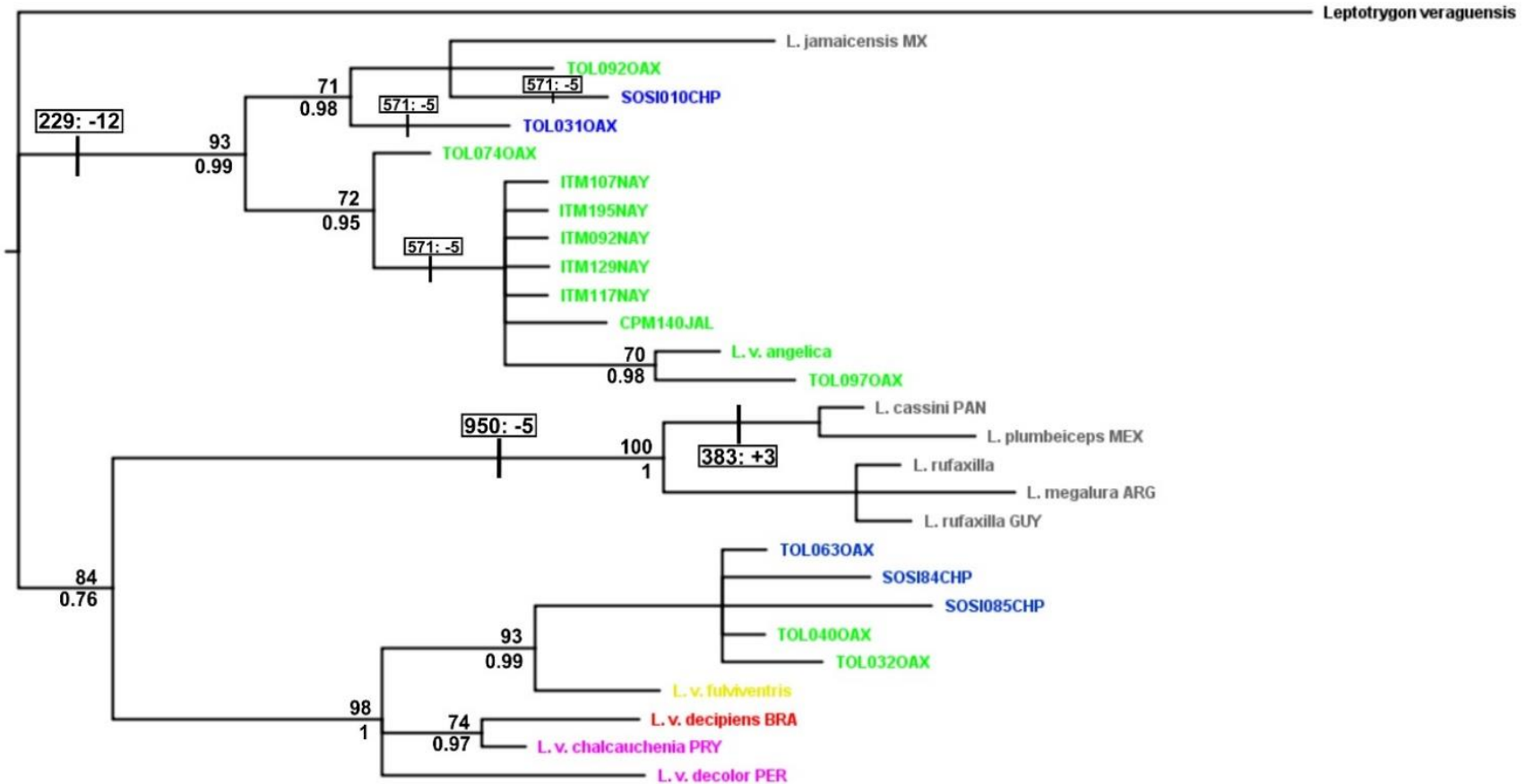
Figure S1. Nuclear phylogeny (β-fibint 7). The upper values of the nodes correspond to the Bootstrap value (ML) and the lower values to the posterior probability (IB). In rectangles the indels present in the sequences and their length are highlighted.

Figure S2. Polygons representing M per lineage as obtained in Grinnell v.0.0.21 (Machado-Stredel et al., 2021), green (NA), blue (NCA) and Yellow (YUC).
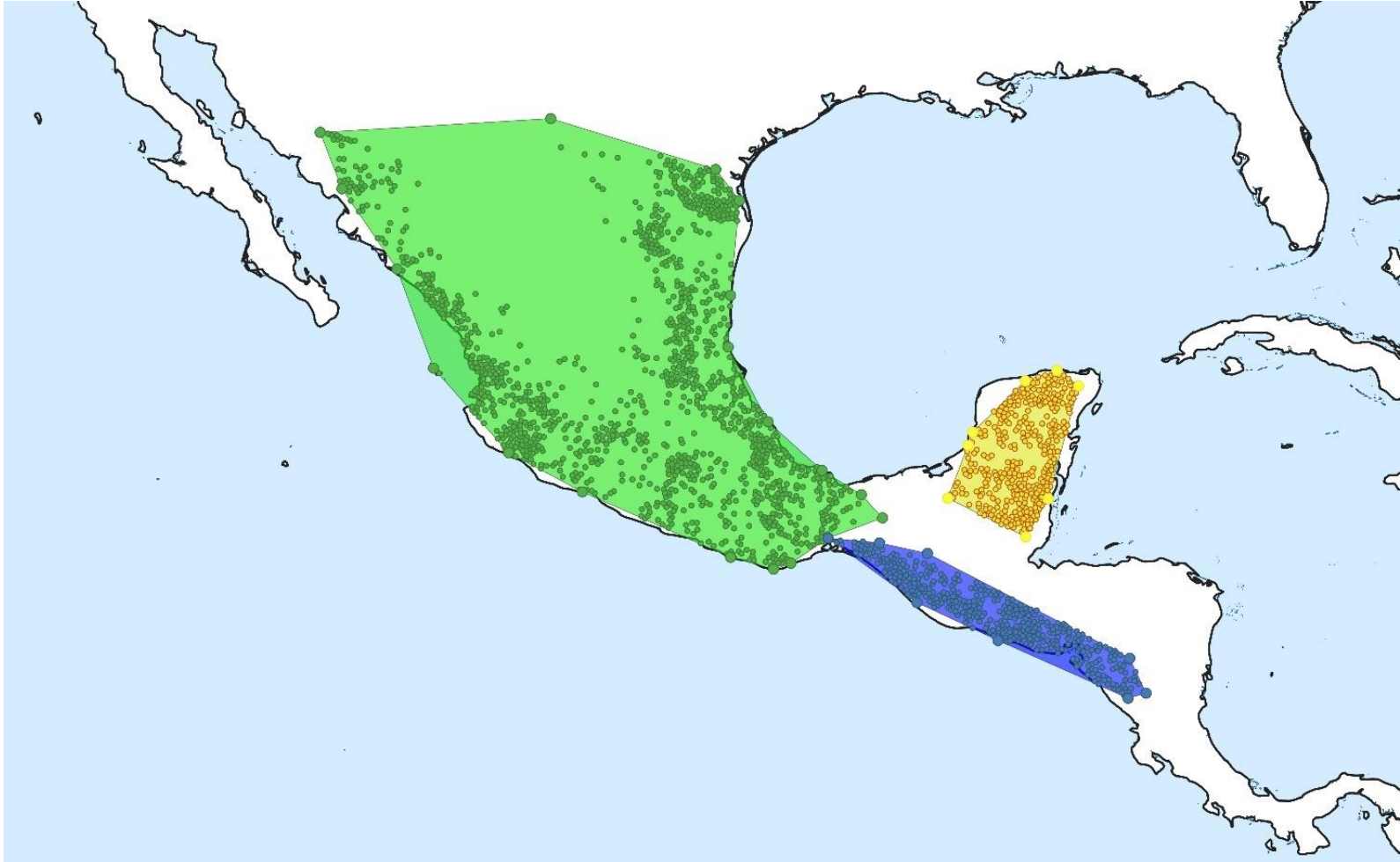
Figure S3. Polygons drawn to select the occurrence points of each lineage, green (NA), blue (NCA) and Yellow (YUC).
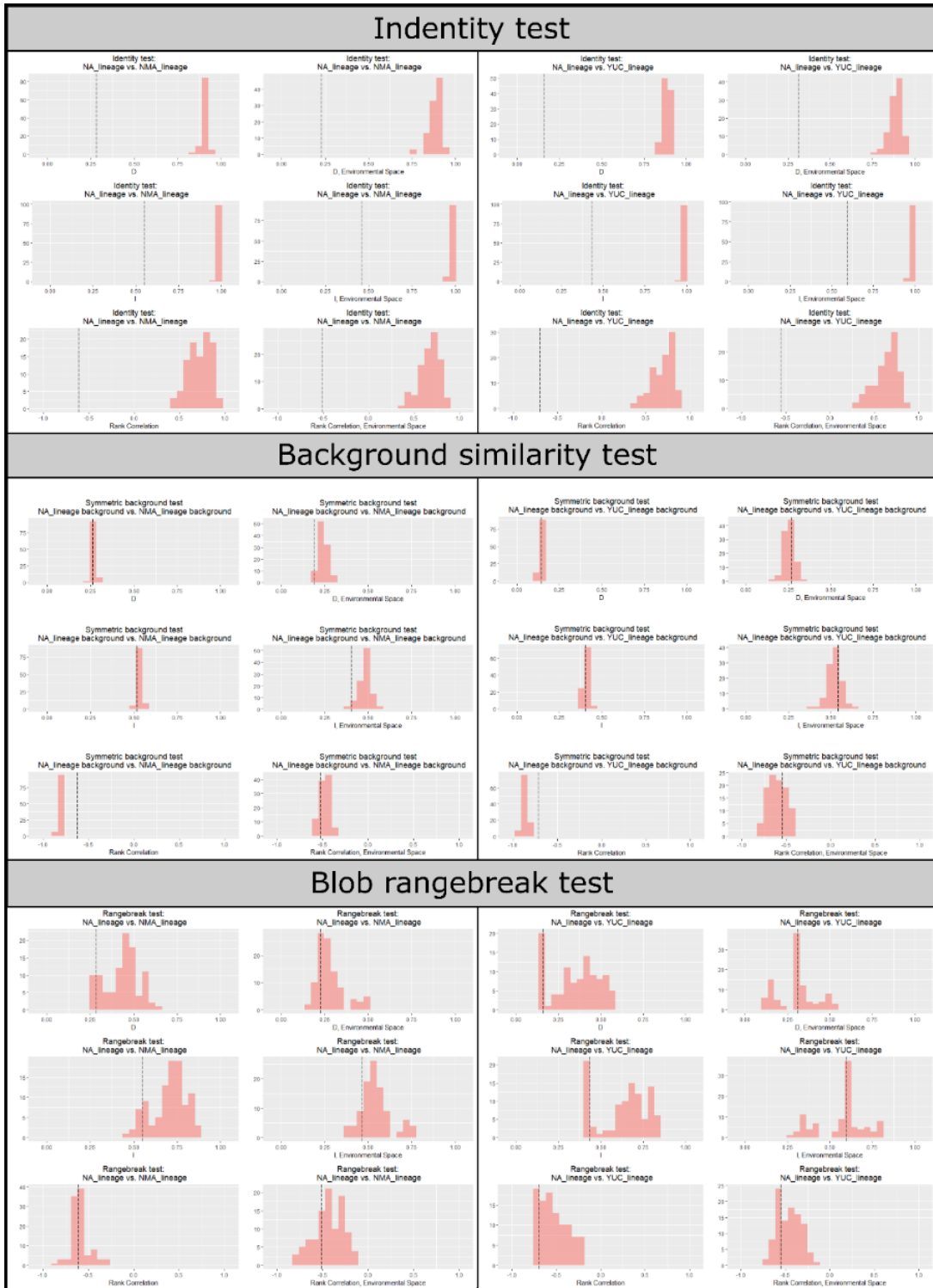
Figure S4. Graphic results of the *identity*, *background*, and *rangebreak blob tests* of the NA vs. NCA (left) and NA vs YUC (right) lineages, the dotted line represents the empirical data, and the bar graphs represent the null hypothesis of pseudoreplicates.
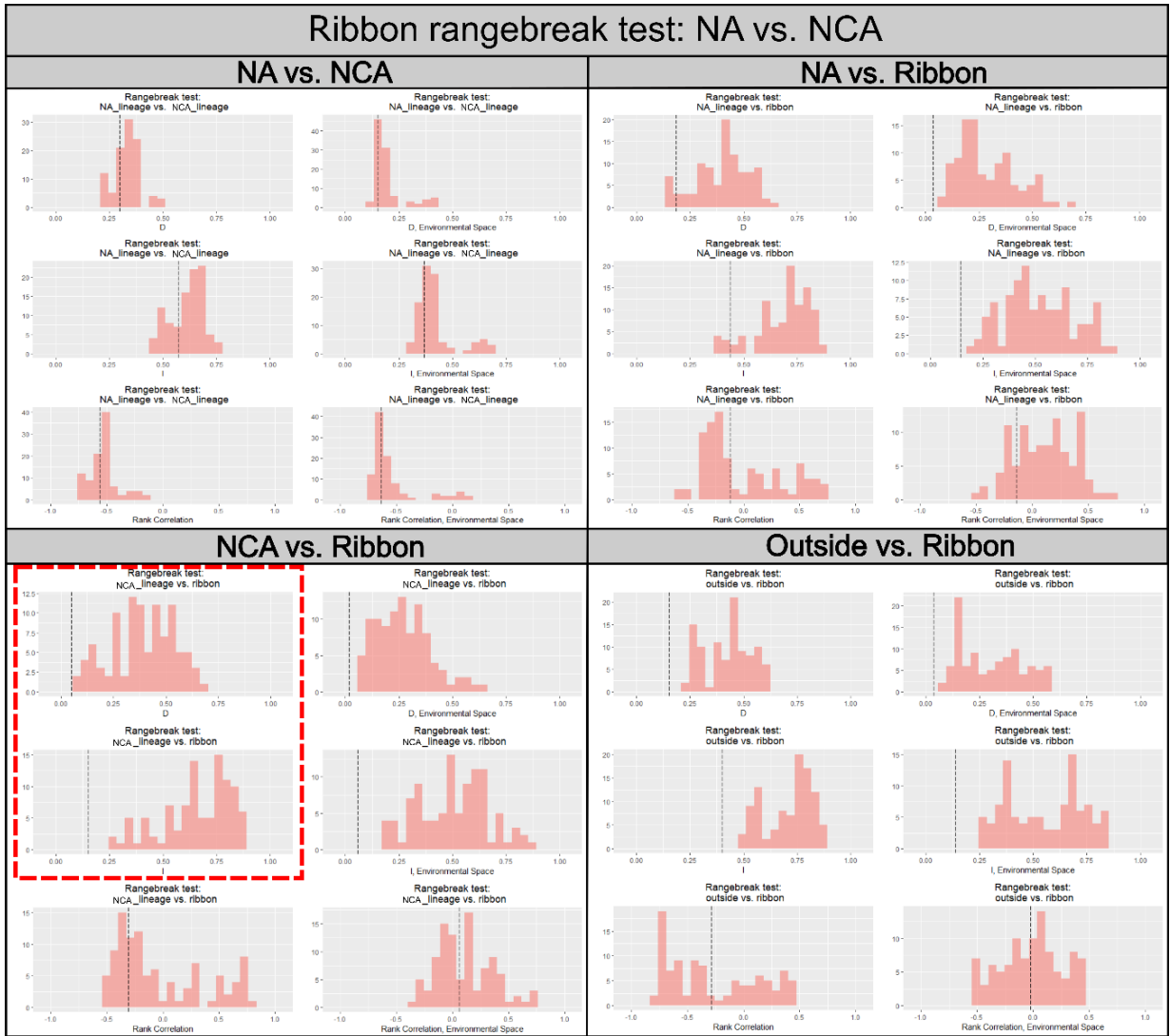
Figure S5. Graphical results of the *ribbon rangebreak test* between the sympatric NA and NCA lineages, the null hypothesis was only rejected when comparing the NCA vs. the ribbon (dotted red box).
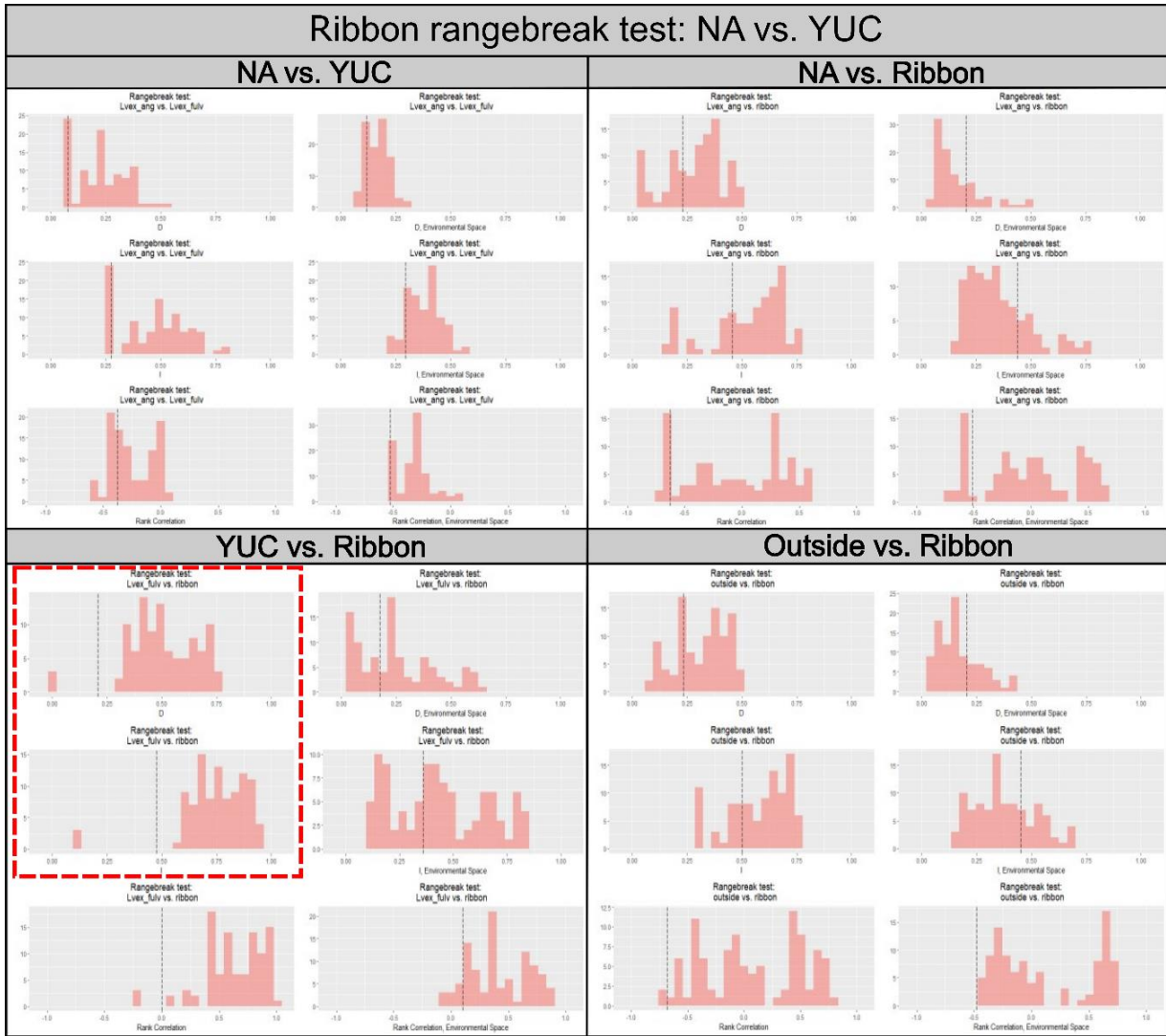
Figure S6. Graphical results of the *ribbon rangebreak test* between the NA and YUC lineages, the null hypothesis was only rejected when comparing the YUC vs. the ribbon (dotted red box).

Taxon	Collection number	Location	ND2	COI	β-fibint 7
L. v. angelica	BAL 284	Guerrero, San Miguel Tecuiciapan, Tlalalpa	X	X	
L. v. angelica	BORJA 29	Chiapas, Coapilla 4 km al N	X		
L. v. angelica	CHAM 08 05	Jalisco, Chamela (Centro Vacacional Sección 47 SNTE)	X		
L. v. angelica	CHAM 08 12	Jalisco, Chamela (Centro Vacacional Sección 47 SNTE)	X	X	
L. v. angelica	CHIMA 280	Oaxaca, San Isidro La Gringa, a 1 km SE de San Francisco La Paz	X		
Leptotila verreauxi	CHIS 369	Chiapas, Pijijiapan, Rancho La Industria	X	X	
Leptotila verreauxi	CHIS 88	Chiapas, Pijijiapan, Rancho Lluvia de Oro 900 m NW de Ranchería las Guadalupes	X		
L. v. angelica	CONACYT 1011	Guerrero, El Carmen 2km NE	X		
L. v. angelica	CONACYT 1116	Tamaulipas, Zona arqueológica El Sabinito, 5 km NW de El Sabinito	X		
L. v. angelica	CONACYT 1125	Tamaulipas, Zona arqueológica El Sabinito, 5 km NW de El Sabinito	X	X	
L. v. angelica	CONACYT 1483	Oaxaca, Nizanda, Camino a las Sabanas	X	X	
L. v. angelica	CONACYT 430	San Luis Potosí, San Nicolás de los Montes en el Río	X		
L. v. angelica	CPM 071	Jalisco, El Tuito, Rancho Los Cuates	X	X	
L. v. angelica	CPM 084	Jalisco, El Tuito, Rancho Los Cuates	X	X	
L. v. angelica	CPM 103	Jalisco, El Tuito, Rancho Los Cuates	X	X	
L. v. angelica	CPM 140	Jalisco, Autlán de Navarro, Ayutita	X	X	X
L. v. angelica	CPM 177	Nayarit, Tepic, Salazares	X	X	
L. v. angelica	CPM 295	Oaxaca, Parque Nacional Huatulco, Sendero El sabanal	X	X	
L. v. angelica	CSW 8127	Sinaloa, El Fuerte 22 km SW, 4 km NW of Ejido Tesila	X	X	
L. v. angelica	CSW 8137	Sinaloa, El Fuerte 22 km SW, 4 km NW of Ejido Tesila	X	X	
L. v. fulviventris	GES 387	Campeche, La Reforma, 20 Km W Silvituc	X		
L. v. angelica	HGO-SLP 128	San Luis Potosí, Tanlacut	X		
L. v. angelica	INECOL 097	Veracruz, El Haya, Instituto de Ecología	X		
L. v. angelica	INECOL 116	Veracruz, El Haya, Instituto de Ecología	X		
L. v. angelica	INECOL 117	Veracruz, El Haya, Instituto de Ecología	X		
L. v. capitalis	ITM 092	Nayarit, Islas Marías, Isla María Magdalena, 1er Campamento (base)	X	X	X
L. v. capitalis	ITM 107	Nayarit, Islas Marías, Isla María Magdalena, 1er Campamento (base)	X	X	X
L. v. capitalis	ITM 117	Nayarit, Islas Marías, Isla María Madre, campamento El Zacatal	X	X	X

L. v. capitalis	ITM 129	Nayarit, Islas Marías, Isla María Madre, campamento El Zacatal	X		X
L. v. capitalis	ITM 195	Nayarit, Islas Marías, Isla María Magdalena, 1er Campamento (base)	X		X
L. v. capitalis	ITM 254	Nayarit, Islas Marías, Isla María Madre, campamento El Zacatal	X		
L. v. angelica	LAB 015	Guerrero, Xocomanatlán	X		
Leptotila verreauxi	MMF 283	Not specified	X		
L. v. bangsi	SOSI 010	Chiapas, Reserva El Silencio	X	X	X
L. v. bangsi	SOSI 084	Chiapas, Reserva El Silencio	X	X	X
L. v. bangsi	SOSI 085	Chiapas, Reserva El Silencio	X	X	X
L. v. bangsi	SOSI 140	Chiapas, Reserva El Silencio	X		
Leptotila verreauxi	TOL 031	Oaxaca, Ejido La Venta, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 032	Oaxaca, Ejido La Venta, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 040	Oaxaca, Ejido La Venta, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 063	Oaxaca, Ejido La Ventosa, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 074	Oaxaca, Ejido La Ventosa, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 092	Oaxaca, Ejido La Ventosa, Juchitán de Zaragoza	X	X	X
Leptotila verreauxi	TOL 097	Oaxaca, Ejido La Ventosa, Juchitán de Zaragoza	X	X	X
L. v. angelica	URRA 11	Jalisco, El Tuito, Rancho Primavera	X		
L. v. angelica	VGR 961	Sinaloa, Ejido El Naranjo 25 km SW de E l Fuerte	X		
L. v. fulviventris	Y480 025	Yucatán, Ejido Chulbac, La Sabana	X		
L. v. fulviventris	YUC13 103	Yucatán, Río Lagartos, Reserva de la Biosfera Ría Lagartos	X		
L. v. angelica		USA	AF353448	AF279725	AF279715
Leptotila verreauxi		Belice	FJ175693		
Leptotila verreauxi		Panamá	FJ175694		
Leptotila verreauxi		Panamá	FJ175695		
Leptotila verreauxi		Panamá	FJ175696		
Leptotila verreauxi		Venezuela	HM640214	HM640214	
L. v. decipiens		Brasil	HQ993539	HQ993515	AY443684
L. v. chalcauchenia		Paraguay	HQ993540	HQ993516	HQ993559
L. v. fulviventris		México	HQ993546	HQ993525	HQ993562

L. v. decolor	Perú	HQ993547	HQ993526	HQ993563
Leptotila verreauxi	Venezuela	NC_015190	NC_015190	
Leptotila rufaxilla	N/A	AF251546	AF353494	AF182665
Leptotila rufaxilla	N/A	EF373340		
Leptotila rufaxilla	Guyana	HQ993541	HQ993517	HQ993560
Leptotila plumbeiceps	México	HQ993544	AF279727	AF279717
Leptotila megalura	Argentina	HQ993545	HQ993520	AF182664
Leptotila jamaicensis	México	HQ993543	AF279726	AF279716
Leptotila cassini	Belice	FJ175701		
Leptotila cassini	Panamá	HQ993542	HQ993518	HQ993561
Geotrygon veraguensis	Panamá	HQ993538	HQ993514	HQ993558

Table S1. Tissue samples with geographic data and access code in GenBank.

	Partitions	Model
Bayesian Inference	ND2_pos1, ND2_pos2, COI_pos2, COI_pos3, Gene3_FIB7	GTR+I+G
	ND2_pos3, COI_pos1	GTR+G
ML	ND2_pos1, ND2_pos2, COI_pos2, COI_pos3, Gene3_FIB7	GTR
	ND2_pos3, COI_pos1	GTR

Table S2. Molecular substitution models and their partitions.

	n	bp	S	h (SD)	H_d	π (SD)	Tajima's D	Fu and Li's D	P
L. verreauxi	18	2422	123	17 (0.021)	0.993	0.01690 (0.00153)	0.53293	-0.16099	P > 0.10
ND2	55	979	85	25 (0.022)	0.926	0.02163 (0.00207)	0.48917	-0.00882	P > 0.10
COI	33	377	32	8 (0.094)	0.581	0.02475 (0.0035)	0.52745	0.41869	P > 0.10
β-fibint 7	21	684	16	13 (0.073)	0.862	0.00486 (0.00060)	-1.09639	-1.88796	P > 0.10
NA	9	2556	19	8 (0.064)	0.972	0.00230 (0.00047)	-0.92864	-0.62263	P > 0.10
ND2	34	988	16	16 (0.051)	0.859	0.00183 (0.00026)	-1.78628	-2.32794	P > 0.10
COI	21	379	0	-	-	-	-	-	-
β-fibint 7	12	713	8	5 (0.163)	0.576	0.00264 (0.00098)	-1.1612	-0.53139	P > 0.10
NCA	5	2482	21	5 (0.016)	1	0.00443 (0.00106)	0.30897	0.44941	P > 0.10
ND2	8	1012	1	2 (0.180)	0.250	0.00025 (0.00018)	-1.05482	-1.12639	P > 0.10
COI	6	378	1	2 (215)	0.333	0.00088 (0.00057)	-0.93302	-0.95015	P > 0.10
β-fibint 7	5	1082	19	5 (0.126)	1	0.00943 (0.00232)	0.46204	0.64786	P > 0.10
YUC									
ND2	5	1021	1	2 (0.237)	0.400	0.00039 (0.00023)	-0.81650	-0.81650	P > 0.10
SCA									
ND2	5	1041	1	2 (0.175)	0.600	0.00058 (0.00017)	1.22474	1.22474	P > 0.10
SA									
ND2	3	1041	17	3 (0.272)	1.000	0.01089 (0.00309)	-	-	-

Table S3. Genetic diversity measurements and neutrality test for each of the *L. verreauxi* populations.

DISCUSIÓN GENERAL Y CONCLUSIONES

Las barreras biogeográficas desempeñan un papel fundamental en a la diversificación de la biodiversidad y la especiación, al modificar la distribución espacial de los organismos y promover el aislamiento genético. Sin embargo, algunas de estas barreras son más difíciles de observar, ya que pueden ser resultado de procesos ecológicos y no por barreras físicas evidentes que limiten la dispersión (Glor y Warren, 2011).

Los resultados de mis análisis filogeográficos, utilizando a *Leptotila verreauxi* como modelo de estudio, revelan patrones emergentes que se han observado en diferentes taxa dentro de la región del Istmo de Tehuantepec. Se observó un patrón de diferenciación oeste-este entre las poblaciones, así como la presencia de zonas de contacto. Estos resultados coinciden con estudios previos a lo largo de la costa del Pacífico mexicano y el IT, que han revelado patrones evolutivos inesperados (por ejemplo, Arcangeli *et al*., 2018; Castillo-Chora *et al*., 2021; Llanes-Quevedo *et al*., 2022; Sánchez-González *et al*., 2021; Sánchez-González *et al*., 2022), Se han identificado especies o poblaciones con preferencia de tierras bajas que muestran una divergencia profunda a pesar de tener una distribución continua a lo largo de toda el área.

Los resultados sugieren que la hipótesis filogenética derivada de este estudio no coincide con las subespecies reconocidas actualmente mediante taxonomía fenética tradicional. Además, se observó que los grupos distribuidos al oeste (NA) y al este (NA-YUC) del IT presentan una divergencia profunda, entre NA-NCA (3,8%) y entre NA-YUC (3,6%), lo cual supera los umbrales tradicionales para el reconocimiento de especies, con niveles de divergencia mayores al 2.7% (Fuchs *et al*., 2021; Hebert *et al*., 2004; Seutin *et al*., 1995). Esto sugiere la necesidad de revisar su estado taxonómico, con la posibilidad de que algunos de los linajes con niveles altos de diferenciación como es el caso de NA y NCA-YUC, reciban el estatus de especies. También se destaca el papel del IT como una barrera significativa que ha promovido la diferenciación en taxa de tierras bajas. Además, los resultados sugieren la presencia de una zona de contacto para los linajes NA y NCA al sur de la región, ubicada en los bosques secos estacionales de las estribaciones de la vertiente del Pacífico de la Sierra del Tolistoque, Oaxaca.

Según los datos obtenidos en este estudio, durante el Mioceno Tardío, *L. verreauxi* se separó de otras especies de su mismo género debido a los cambios climáticos que dividieron los bosques secos y húmedos en Mesoamérica. Estos eventos de divergencia son similares a

la diferenciación observada en otros grupos de aves con hábitat similar durante el mismo tiempo, como *Melanerpes* (Llanes-Quevedo *et al.*, 2022; Navarro-Sigüenza *et al.*, 2017). Posteriormente, durante el Plioceno Tardío e inicios del Pleistoceno, hace unos 2,6 millones de años, ocurrió la diferenciación de linajes dentro de *L. verreauxi,* al oeste (NA) y al este del IT (NCA-YUC, SCA-SA). Estos cambios climáticos también modificaron la vegetación en toda la región, separando las conexiones entre los ecosistemas que antes estaban continuos en pequeños parches (*e. g.*, Castillo-Chora *et al.* 2021), reduciendo el flujo de genes entre las poblaciones (Sánchez-González *et al.*, 2021; 2022).

La fecha de separación entre los grupos al oeste y este del IT coincide con la formación de una vía marítima hipotética que cruzó la región hace 2-3 millones de años (Barrier *et al.*, 1998). Sin embargo, debido a que esta teoría ha sido cuestionada (Mulcahy *et al.*, 2006; Wyatt Durham *et al.*, 1955), hipótesis alternativas, como la divergencia de nicho ecológico, la reducción del área de distribución en pequeños parches relacionado con los cambios climáticos pleistocénicos y el papel de las diferencias ambientales como límite biogeográfico han sido propuestas (Castillo-Chora *et al.* 2021, Sánchez-González *et al.*, 2022, Butler *et al.*, 2023).

Los resultados indican la existencia de una zona de contacto para los linajes NA y NCA al sur de la IT, donde los individuos genéticamente divergentes coexisten. Las fluctuaciones climáticas del Pleistoceno promovieron la divergencia de los grupos oeste y este a través del Istmo, y tras la desaparición de la barrera, las poblaciones se expandieron hacia áreas ecológicamente adecuadas. Sin embargo, las diferencias ambientales y las interacciones biológicas entre taxa con nichos similares (por ejemplo, exclusión competitiva) pueden frenar el proceso de recolonización (Anderson *et al.*, 2002), lo que a su vez mantiene la diferenciación en la zona de contacto secundario.

La similitud entre los nichos ecológicos de NA y NCA puede explicar su distribución simpátrica en el sur del IT. Según las pruebas de *blob* y *ribbon-rangebreak*, las diferencias ambientales en el IT no parecen representar una barrera ambiental abrupta para la dispersión de las poblaciones de *L. verreauxi* entre hábitats. No obstante, los resultados sugieren que las zonas de contacto pueden tener áreas con condiciones menos adecuadas para la dispersión. Las poblaciones de NCA parecen ser menos tolerantes a las condiciones climáticas de los bosques secos en la vertiente del Pacífico, lo que limita su dispersión hacia el oeste. Por otro lado, las poblaciones de NA son tolerantes tanto a las condiciones húmedas como a las secas,

pero otros factores, como las interacciones biológicas, deben considerarse en el mantenimiento la limitada zona de contacto secundaria.

Estos hallazgos sugieren que la zona de contacto secundaria se ha mantenido debido a una adecuación ecológica limitada para NCA al oeste de IT, mientras que al este, la divergencia puede haberse mantenido a través de interacciones ecológicas o movimientos estacionales. Aunque este estudio no cuenta con suficientes datos genéticos sobre las poblaciones al norte de IT, que se superponen geográficamente, es posible que la diferenciación entre los linajes NA y YUC, sin barreras conspicuas, se mantenga debido al papel de los pantanales de la desembocadura del río Usumacinta actuando como límite biogeográfico.

En términos generales, el Istmo de Tehuantepec es reconocido tradicionalmente como un límite geográfico para algunas familias de aves norteamericanas (Navarro-Sigüenza *et al*., 2014), así como un impulsor de la especiación y diferenciación ecológica para las aves de montaña. Sin embargo, su papel como barrera para las aves de tierras bajas no está del todo claro (ver Binford, 1989). Es importante considerar cuidadosamente los patrones de divergencia en las poblaciones de tierras bajas en regiones con una historia biótica dinámica y compleja, donde los cambios en las condiciones ecológicas probablemente han promovido la divergencia. Esto se sugiere tanto en los linajes de *L. verreauxi* como en otros taxa de aves en el IT (Castillo-Chora *et al*. 2021; Sánchez-González *et al*, 2021; Llanes-Quevedo *et al*., 2022; Sánchez-González *et al*, 2022).

REFERENCIAS BIBLIOGRÁFICAS

Anderson, R. P., Peterson, A. T., y Gómez-Laverde, M. (2002). Using Niche-Based GIS Modeling to Test Geographic Predictions of Competitive Exclusion and Competitive Release in South American Pocket Mice. *Oikos*, *98*(1), 3–16.

Arcangeli, J., Light, J. E., y Cervantes, F. A. (2018). Molecular and morphological evidence of the diversification in the gray mouse opossum, Tlacuatzin canescens (Didelphimorphia), with description of a new species. *Journal of Mammalogy*, *99*(1), 138–158. https://doi.org/10.1093/jmammal/gyx173

Barber, B. R., y Klicka, J. (2010). Two pulses of diversification across the Isthmus of Tehuantepec in a montane Mexican bird fauna. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1694), 2675–2681. https://doi.org/10.1098/rspb.2010.0343

Barrier, E., Velasquillo, L., Chavez, M., & Gaulon, R. (1998). Neotectonic evolution of the Isthmus of Tehuantepec (southeastern Mexico). *Tectonophysics*, *287*(1–4), 77–96. https://doi.org/10.1016/S0040-1951(98)80062-0

Benham, P. M., y Cheviron, Z. A. (2019). Divergent mitochondrial lineages arose within a large, panmictic population of the Savannah sparrow (Passerculus sandwichensis). *Molecular Ecology*, 0–3. https://doi.org/10.1111/mec.15049

Binford, L. C. (Laurence C. (1989). *A distributional survey of the birds of the Mexican state of Oaxaca*. American Ornithologists' Union.

Butler, B. O., Smith, L. L., y Flores-villela, O. (2023). Molecular Phylogenetics and Evolution Phylogeography and taxonomy of Coleonyx elegans Gray 1845 (Squamata: Eublepharidae) in Mesoamerica: The Isthmus of Tehuantepec as an environmental barrier. *Molecular Phylogenetics and Evolution*, *178*(August 2022), 107632. https://doi.org/10.1016/j.ympev.2022.107632

Castillo-Chora, V. D. J., Sánchez-González, L. A., Mastretta-Yanes, A., Prieto-Torres, D. A., y Navarro-Sigüenza, A. G. (2021). Insights into the importance of areas of climatic stability in the evolution and maintenance of avian diversity in the Mesoamerican dry forests. *Biological Journal of the Linnean Society*, *2000*, 1–18. https://doi.org/10.1093/biolinnean/blaa202

Cobos, M. E., Townsend Peterson, A., Barve, N., y Osorio-Olvera, L. (2019). Kuenm: An R package for detailed development of ecological niche models using Maxent. *PeerJ*, *2019*(2), 1–15. https://doi.org/10.7717/peerj.6281

Dansgaard, W., Johnsen, S. J., Clausen, H. B., Dahl-Jensen, D., Gundestrup, N. S., Hammer, C. U., Hvidberg, C. S., Steffensen, J. P., Sveinbjörnsdottir, A. E., Jouzel, J., & Bond, G. (1993). Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature*, *364*(6434), 218–220. https://doi.org/10.1038/364218a0

Edwards, E. P., y Lea, R. B. (1955). Birds of the Monserrate Area, Chiapas, Mexico. *The Condor*, *57*(1), 31–54. https://doi.org/10.2307/1364696

Ferrusquia-Villafrance, I. (1993). Geology of Mexico: A synopsis. *Biological Diversity of Mexico: Origins and Distribution*, 3–108.

Friedmann, H., Griscom, L., y Moore, R. T. (1950). Distributional Check-List of the Birds of Mexico. Part I. In *Bird-Banding*. https://doi.org/10.2307/4510250

Fuchs, J., Bowie, R. C. K., Melo, M., Boano, G., Pavia, M., y Fjeldså, J. (2021). Phylogeographical history of the Olive Woodpecker Dendropicos griseocephalus, a species widely distributed across Africa. *Ibis*, *163*(2), 417–428. https://doi.org/10.1111/ibi.12875

Giese, J. C., K. M. Hogan, y Mathewson H. A. (2020). White-tipped Dove (Leptotila verreauxi), version 1.0. En Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whtdov.01

Gill, F., Donsker, D., y Rasmussen, P. (Eds). (2021). *IOC World Bird List (v13.1)*. https://doi.org/10.14344/IOC.ML.13.1.

Glor, R. E., & Warren, D. (2011). Testing ecological explanations for biogeographic boundaries. *Evolution*, *65*(3), 673–683. https://doi.org/10.1111/j.1558-5646.2010.01177.x

Gray, L. N., Barley, A. J., Poe, S., Thomson, R. C., Nieto-Montes de Oca, A., y Wang, I. J. (2019). Phylogeography of a widespread lizard complex reflects patterns of both geographic and ecological isolation. *Molecular Ecology*, *28*(3), 644–657. https://doi.org/10.1111/mec.14970

Hebert, P. D. N., Stoeckle, M. Y., Zemlak, T. S., y Francis, C. M. (2004). Identification of birds through DNA barcodes. *PLoS Biology, 2*(10), e312. https://doi.org/10.1371/journal.pbio.0020312

Hogan, K. M. (1999). White-tipped Dove (Leptotila verreauxi). In A. Poole y F. Gill (Eds.), *The Birds of North America No. 436*. The Birds of North America, Inc.

Hogner, S., Laskemoen, T., Lifjeld, J. T., Porkert, J., Kleven, O., Albayrak, T., Kabasakal, B., y Johnsen, A. (2012). Deep sympatric mitochondrial divergence without reproductive isolation in the common redstart phoenicurus phoenicurus. *Ecology and Evolution*, *2*(12), 2974–2988. https://doi.org/10.1002/ece3.398

Howell, S. N. G., y Webb, Sophie. (1995). A Guide to the Birds of Mexico and Northern Central America. In *Oxford University Press*. Oxford University Press.

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Llanes-Quevedo, A., Mastretta-Yanes, A., Sánchez-González, L. A., Castillo-Chora, V. J., y Navarro-Sigüenza, A. G. (2022). The tangled evolutionary history of a long-debated Mesoamerican taxon: The Velazquez Woodpecker (Melanerpes santacruzi, Aves: Picidae). *Molecular Phylogenetics and Evolution*, *170*, 107445. https://doi.org/10.1016/j.ympev.2022.107445

Machado-Stredel, F., Cobos, M. E., y Peterson, A. T. (2021). A simulation-based method for selecting calibration areas for ecological niche models and species distribution models. *Frontiers of Biogeography*, *0*(0), 0–23. https://doi.org/10.21425/f5fbg48814

Mastretta-Yanes, A., Moreno-Letelier, A., Piñero, D., Jorgensen, T. H., & Emerson, B. C. (2015). Biodiversity in the Mexican highlands and the interaction of geology, geography and climate within the Trans-Mexican Volcanic Belt. *Journal of Biogeography*, *42*(9), 1586–1600. https://doi.org/10.1111/jbi.12546

Mayewski, P. A., Rohling, E. E., Curt Stager, J., Karlén, W., Maasch, K. A., David Meeker, L., Meyerson, E. A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R. R., y Steig, E. J. (2004). Holocene climate variability. *Quaternary Research*, *62*(3), 243–255. https://doi.org/10.1016/j.yqres.2004.07.001

Mulcahy, D. G., Morrill, B. H., y Mendelson III, J. R. (2006). Historical biogeography of lowland species of toads (Bufo) across the Trans-Mexican Neovolcanic Belt and the Isthmus of Tehuantepec. *Journal of Biogeography*, *33*(11), 1889–1904.

Navarro-Sigüenza, A. G., Rebón-Gallardo, M. F., Gordillo-Martínez, A., Peterson, A. T., Berlanga-García, H., y Sánchez-González, L. A. (2014). Biodiversidad de aves en México. *Revista Mexicana de Biodiversidad*, *85*(SUPPL.), 476–495. https://doi.org/10.7550/rmb.41882

Navarro-Sigüenza, A. G., Vázquez-Miranda, H., Hernández-Alonso, G., García-Trejo, E. A., y Sánchez-González, L. A. (2017). Complex biogeographic scenarios revealed in the diversification of the largest woodpecker radiation in the New World. *Molecular Phylogenetics and Evolution*, *112*, 53–67. https://doi.org/10.1016/j.ympev.2017.04.013

Ornelas, J. F., Sosa, V., Soltis, D. E., Daza, J. M., González, C., Soltis, P. S., Gutiérrez-Rodríguez, C., de los Monteros, A. E., Castoe, T. A., Bell, C., y Ruiz-Sanchez, E. (2013). Comparative Phylogeographic Analyses Illustrate the Complex Evolutionary History of Threatened Cloud Forests of Northern Mesoamerica. *PLoS ONE*, *8*(2), 56283. https://doi.org/10.1371/journal.pone.0056283

Parkinson, C. L., Zamudio, K. R., y Greene, H. W. (2000). Phylogeography of the pitviper clade Agkistrodon: Historical ecology, species status, and conservation of cantils. *Molecular Ecology*, *9*(4), 411–420. https://doi.org/10.1046/J.1365-294X.2000.00854.X

Peterson, A. T., Soberón, J., y Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, *285*(5431), 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Peterson, A. Townsend. (2012). perspective: Phylogeography is not enough: The need for multiple lines of evidence. *Frontiers of Biogeography*, *1*(1). https://doi.org/10.21425/f5fbg12232

Peterson, A. Townsend, & Ammann, C. M. (2013). Global patterns of connectivity and isolation of populations of forest bird species in the late Pleistocene. *Global Ecology and Biogeography*, *22*(5), 596–606. https://doi.org/10.1111/geb.12010

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., y Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*(7), 887–893. https://doi.org/10.1111/ecog.03049

Sánchez-González, L. A., Castillo-Chora, V. J., Navarro-Sigüenza, A. G., y Arbeláez-Cortés, E. (2021). Diversification and secondary contact in the magpie-jays (Calocitta) throughout the pacific lowlands of Mesoamerica. *Journal of Zoological Systematics and Evolutionary Research*, *59*(8), 2371–2386. https://doi.org/10.1111/jzs.12571

Sánchez-González, L. A., Cayetano, H., Prieto-Torres, D. A., Rojas-Soto, O. R., y Navarro-Sigüenza, A. G. (2022). The role of ecological and geographical drivers of lineage diversification in the Squirrel cuckoo Piaya cayana in Mexico: A mitochondrial DNA perspective. *Journal of Ornithology 2022*, *1*, 1–17. https://doi.org/10.1007/S10336-022-02008-W

Seutin, G., Ratcliffe, L. M., y Boag, P. T. (1995). Mitochondrial DNA Homogeneity in the Phenotypically Diverse Redpoll Finch Complex (Aves: Carduelinae: Carduelis flammea-hornemanni). *Evolution*, *49*(5), 962–973. https://doi.org/10.2307/2410418

Shackleton, N. J. (2000). The 100,000-Year Ice-Age Cycle Identified and Found to Lag Temperature, Carbon Dioxide, and Orbital Eccentricity. *Science*, *289*(5486), 1897–1902.

Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H. H., y Warren, D. (2019). Niche Estimation Above and Below the Species Level. *Trends in Ecology and Evolution*, *34*(3), 260–273. https://doi.org/10.1016/j.tree.2018.10.012

Sosa-López, J. R., González, C., y Navarro-Sigüenza, A. G. (2013). Vocal Geographic Variation In Mesoamerican Common Bush Tanagers (Chlorospingus ophthalmicus). *The Wilson Journal of Ornithology*, *125*(1), 24–33. https://doi.org/10.1676/12-051.1

Tominaga, K., Watanabe, K., Kakioka, R., Mori, S., y Jeon, S. R. (2009). Two highly divergent mitochondrial DNA lineages within Pseudogobio esocinus populations in central Honshu, Japan. *Ichthyological Research*, *56*(2), 195–199. https://doi.org/10.1007/s10228-008-0071-0

Tsai, W. L. E., Mota-Vargas, C., Rojas-Soto, O., Bhowmik, R., Liang, E. Y., Maley, J. M., Zarza, E., y McCormack, J. E. (2019). Museum genomics reveals the speciation history of Dendrortyx wood-partridges in the Mesoamerican highlands. *Molecular Phylogenetics and Evolution*, *136*, 29–34. https://doi.org/10.1016/j.ympev.2019.03.017

Venkatraman, M. X., Deraad, D. A., Tsai, W. L. E., Zarza, E., Zellmer, A. J., Maley, J. M., y McCormack, J. E. (2019). Cloudy with a chance of speciation: Integrative taxonomy reveals

extraordinary divergence within a Mesoamerican cloud forest bird. *Biological Journal of the Linnean Society*, *126*(1), 1–15. https://doi.org/10.1093/biolinnean/bly156

Warren, D. L., Cardillo, M., Rosauer, D. F., & Bolnick, D. I. (2014). Mistaking geography for biology: Inferring processes from species distributions. *Trends in Ecology and Evolution*, *29*(10), 572–580. https://doi.org/10.1016/j.tree.2014.08.003

Warren, D. L., Matzke, N. J., Cardillo, M., Baumgartner, J. B., Beaumont, L. J., Turelli, M., Glor, R. E., Huron, N. A., Simões, M., Iglesias, T. L., Piquet, J. C., y Dinnage, R. (2021). ENMTools 1.0: An R package for comparative ecological biogeography. *Ecography*, *44*(4), 504–511. https://doi.org/10.1111/ecog.05485

Wogau, K. H., Arz, H. W., Böhnel, H. N., Nowaczyk, N. R., y Park, J. (2019). High resolution paleoclimate and paleoenvironmental reconstruction in the Northern Mesoamerican Frontier for Prehistory to Historical times. *Quaternary Science Reviews*, *226*, 106001. https://doi.org/10.1016/j.quascirev.2019.106001

Wyatt Durham, J., Arellano, A. R. V., y Peck, J. H., JR. (1955). Evidence for no cenozoic Isthmus of Tehuantepec seaways. *GSA Bulletin*, *66*(8), 977–992. https://doi.org/10.1130/0016-7606(1955)66[977:EFNCIO]2.0.CO;2

Xiao, J. H., Wang, N. X., Murphy, R. W., Cook, J., Jia, L. Y., y Huang, D. W. (2012). Wolbachia infection and dramatic intraspecific mitochondrial DNA divergence in a fig wasp. *Evolution*, *66*(6), 1907–1916. https://doi.org/10.1111/j.1558-5646.2011.01561.x

Zarza, E., Reynoso, V. H., y Emerson, B. C. (2008). Diversification in the northern neotropics: Mitochondrial and nuclear DNA phylogeography of the iguana Ctenosaura pectinata and related species. *Molecular Ecology*, *17*(14), 3259–3275. https://doi.org/10.1111/j.1365-294X.2008.03826.x