



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

(PROYECTO)

**DISTRIBUCIÓN ECOLÓGICA Y GEOGRÁFICA DE AVES MESOAMERICANAS
DURANTE EL CUATERNARIO TARDÍO: UNA APROXIMACIÓN PALEONTOLÓGICA**

TESIS

(POR ARTÍCULO CIENTÍFICO)

**The role of ecological niche conservatism in the evolution of bird distributional patterns
in Mesoamerican seasonally dry tropical forests**

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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CIUDAD UNIVERSITARIA, CD. MX., NOVIEMBRE, 2023



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COORDINACIÓN GENERAL DE ESTUDIOS DE POSGRADO
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Presente.

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **11 de septiembre 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 alumno **CHAN PAK TSUN** con número de cuenta **309019459** por la modalidad de graduación de **tesis por artículo científico** titulado: **“The role of ecological niche conservatism in the evolution of bird distributional patterns in Mesoamerican seasonally dry tropical forests”**, que es producto del proyecto realizado en la maestría que lleva por título **“DISTRIBUCIÓN ECOLÓGICA Y GEOGRÁFICA DE AVES MESOAMERICANAS DURANTE EL CUATERNARIO TARDÍO: UNA APROXIMACIÓN PALEONTOLÓGICA”** 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 20 de octubre de 2023

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RESUMEN

Los bosques secos caducifolios tropicales mesoamericanos son considerados centros de diversificación para la avifauna debido a su compleja historia biogeográfica y ecológica. Sin embargo, la evolución y mantenimiento de la distribución de especies asociadas a estos bosques sigue siendo poco estudiada. En este trabajo, evaluamos el papel de los nichos ecológicos en la evolución de la distribución de algunas aves endémicas de estos bosques. Estimamos la paleodistribución de seis especies de aves endémicas de bosques secos de la península de Yucatán (PY); especies actualmente endémicas de la Vertiente del Pacífico Mesoamericano (VPM), pero con registro fósil del pleistoceno en la PY; y especies alopátricas en ambas áreas. Simulamos especies virtuales (EV) que coincidieron con cada uno de estos patrones de distribución asumiendo que representan la distribución esperada de especies endémicas para cada parche. Para probar la hipótesis del conservadurismo de nicho, realizamos una prueba de similitud de nicho entre los parches representados por las EV, y entre cada especie con su contraparte distribucional virtual. Observamos tres patrones principales: i) no hubo conectividad geográfica en el pasado entre las áreas idóneas para los taxones de bosques secos mesoamericanos; ii) las pruebas de nicho entre parches indicaron conservadurismo de nicho, pero no equivalencia, para la mayoría de los casos a pesar del poco solapamiento de nicho y la distancia geográfica; iii) potencial divergencia de nicho entre las aves endémicas de PY con respecto a su contraparte virtual. Por lo tanto, para las aves endémicas de la VPM, nuestros resultados sugieren que su ausencia actual de la PY puede atribuirse a la pérdida de su nicho ambiental (similar al presente) y a los cambios en las condiciones bióticas. Estos resultados proporcionan información relevante sobre el papel de los factores geográficos y ecológicos en la evolución, diversificación y distribución de la avifauna de bosques secos mesoamericanos.

ABSTRACT

Seasonally dry tropical forests (SDTF) in Mesoamerica have been regarded as diversification hotspots for avifauna due to its complex biogeographical and ecological history. However, the evolution and maintenance of its distribution remains poorly understood. Here we assess the role of divergence/conservatism of ecological niches in the distribution evolution of some bird endemics to these forests. Using an ecological niche modelling approach, we estimated the paleodistribution of six bird endemics to Yucatan Peninsula SDTF (YP), endemic to the Mesoamerican Pacific Slope SDTF (MPS) with fossil record in YP, and allopatric in both areas. We simulated virtual species (VS) that matched each of these patterns assuming they represent the expected distribution of species endemic to each patch. To test the hypothesis of niche conservatism, we assessed the niche equivalence/similarity between the patches represented by the VS, and each bird species-VS distributional counterpart. We observed three main patterns: *i*) there were no past geographical connectiveness among suitable areas for taxa across the Mesoamerican SDTFs; *ii*) niche tests between patches indicated niche conservatism, but not equivalence, for most cases in spite of low niche overlap and geographic distance; *iii*) potential niche divergence between endemics birds of YP regarding their VS counterpart. Therefore, for endemic birds of MPS, our results suggest that their current absence from YP can be attributed to losing their similar-to-present environmental niche and changes in biotic conditions. These results provide relevant information about the role of geographical and ecological factors on evolution, diversification, and distribution for Mesoamerican SDTF avifauna.

INTRODUCCIÓN

Los ciclos glaciales-interglaciales que ocurrieron a lo largo del Cuaternario Tardío ejercieron efectos profundos sobre la biodiversidad neotropical (Awise & Walker, 1998; Barnosky et al., 2004; Ferrusquía-Villafranca et al., 2009; Hewitt, 2004; Johnson & Cicero, 2004). Estas fluctuaciones estuvieron marcadas por cambios radicales en condiciones ambientales, lo que ocasionó tanto la fragmentación como la unión de áreas de distribución de diversos taxones (Peterson & Lieberman, 2012). Esto se debió en parte a cambios en la vegetación, los cuales favorecieron la expansión y subsecuente fragmentación de poblaciones bióticas asociadas, además de expansiones del área de distribución hacia zonas costeras, debido a la disminución del nivel del mar de entre 80-120 m durante los periodos glaciales (Barnosky et al., 2004; Nakazawa & Peterson, 2015; Peterson & Lieberman, 2012).

Las especies de bosques pudieron responder de cuatro formas ante los cambios climáticos de los periodos glaciales: a) contrayendo sus áreas de distribución hacia áreas climáticamente estables (áreas históricas que permitieron la persistencia de las especies durante periodos glaciales); b) desplazarse por el espacio geográfico en busca de condiciones ambientales idóneas (*niche tracking*), similares a las condiciones de la región donde estaban establecidos (conservadurismo de nicho; Martínez-Meyer et al., 2004; Peterson et al., 2011; Waltari & Guralnick, 2009; Wiens et al., 2010); c) adaptarse *in situ* a las condiciones nuevas, ya sea porque tienen respuestas fisiológicas plásticas o porque adquirieron adaptaciones evolutivas (evolución del nicho; Jezkova et al., 2011; Wiens & Graham, 2005; Wiens et al., 2010); d) extinguirse de su área de distribución debido a que no fueron capaces de desplazarse o adaptarse a las condiciones climáticas nuevas (Wiens & Graham, 2005; Wiens et al., 2010).

Los bosques caducifolios secos neotropicales (SDTF por sus siglas en inglés) son un tipo de vegetación predominante en la mayor parte de los neotrópicos (Arango et al., 2021; Banda et al., 2016; Linares-Palomino, 2011; Pennington et al., 2000). Su origen histórico y su forma fragmentada actual en parches a lo largo del continente ha sido debatido por diversos autores (Arruda et al., 2018; Banda et al., 2016; Capurucho et al., 2020; Collevatti et al., 2013; Corbett et al., 2020; Linares-Palomino, 2011; Pennington et al., 2000; Werneck

et al., 2011). Con respecto a los bosques secos mesoamericanos, se ha sugerido que en el pasado pudieron haber tenido una distribución extendida el cual pudo haber conectado los parches núcleo actuales durante los períodos más áridos y secos de los ciclos glaciales (Contreras-Negrete et al., 2021; Ruiz-Sanchez et al., 2012; Hubbard, 1974; Metcalfe et al., 2000). Si hubiera existido una conexión histórica de estos parches, se esperaría una gran similitud en la composición faunística y florística. Sin embargo, las grandes disimilitudes en la composición de especies de estos parches en el Neotrópico (Montaño-Arias et al., 2018; Ríos-Muñoz & Navarro-Sigüenza, 2012; Banda et al., 2016; Becerra, 2005; Herzog & Kessler, 2002; Montaño-Arias et al., 2018; Oswald et al., 2017; Prieto-Torres et al., 2019a) sugieren que los patrones de composición y diversificación de linajes ocurrieron a través de procesos independientes, a pesar de la aparente continuidad del hábitat (Linares-Palomino, 2011; Pennington et al., 2000; Prieto-Torres et al., 2019a; 2019b; Ríos-Muñoz & Navarro-Sigüenza, 2012; Sánchez-González et al., 2021).

Lo anterior implica una evolución compleja del nicho ecológico y la distribución geográfica de especies que componen estos bosques, el cual sólo ha sido explorada en unos pocos taxones (Hernández-Canchola & León-Paniagua, 2017; Suárez-Mota & Villaseñor, 2020; Castillo-Chora et al., 2021a; Sánchez-González et al., 2021; Widholzer & Prieto-Torres, 2022). Para las aves endémicas de bosques secos mesoamericanos, se han identificado patrones biogeográficos concordantes entre taxones filogenéticamente distantes; sin embargo, la composición biótica de estos patrones ha sido ensamblado a través de diferentes procesos biogeográficos y ecológicos (García-Trejo & Navarro-Sigüenza, 2004; Herzog & Kessler, 2002; Oswald et al., 2017; Ríos-Muñoz & Navarro-Sigüenza, 2012; Trujillo-Arias et al., 2020). Diferentes eventos de divergencia de linajes de aves durante el Último Máximo Glacial (UMG ~22-21 kya) sugieren que los bosques secos de la Vertiente Pacífico Mesoamericano (VPM) ha tenido episodios de fases de aislamiento histórico, en las que algunas aves pudieron haber persistido a las glaciaciones en áreas climáticamente estables, lo que pudo permitir la divergencia genética y persistencia de distintos taxones durante estos periodos (Arbeláez-Cortés et al., 2014; Arbeláez-Cortés & Navarro-Sigüenza, 2013; Castillo-Chora et al., 2021a; Corbett et al., 2020; Sánchez-González et al., 2021; Vázquez-López et al., 2021; Widholzer & Prieto-Torres, 2022). Por otra parte, para las aves

endémicas de los bosques secos de la península de Yucatán (PY), los cambios climáticos de los últimos ciclos glaciales e interglaciales promovieron la fragmentación en la distribución geográfica de varias especies, lo que condujo al aislamiento ambiental y a la eventual divergencia genética de taxones estrechamente relacionados (Barker, 2004; Licona-Vera & Ornelas, 2014; Smith et al., 2018; Williford et al., 2016; Vázquez-López et al., 2021). Sin embargo, aunque los patrones genéticos y biogeográficos han sido bien documentados, son pocos estudios los que se han centrado en la evolución de los nichos ecológicos sin discernir entre el papel que han jugado los factores bióticos en la evolución y mantenimiento de la distribución de las especies.

Existe evidencia de que las aves endémicas de bosques secos mesoamericanos pudieron haber modificado su distribución geográfica. Chan (2018) estudió fósiles de aves datados del Pleistoceno Tardío provenientes de la cueva Loltún en la PY, y asignó algunos de los restos identificados a especies actualmente endémicas de la VPM. Si bien este hallazgo no puede considerarse como evidencia concluyente de una conexión histórica de los bosques secos mesoamericanos (Collevatti et al., 2013), esto sugiere que algunos taxones pudieron tener una distribución más amplia en el pasado (Hubbard, 1974), así como procesos altamente dinámicos de recambios de la distribución geográfica y evolución del nicho ecológico. Por lo tanto, estudiar estas dinámicas ecológicas históricas podría mejorar nuestra comprensión sobre los patrones de biodiversidad de los taxones asociados a bosques secos mesoamericanos (Banda et al., 2016; Becerra, 2005; García-Trejo & Navarro-Sigüenza, 2004; Prieto-Torres et al., 2019a; 2019b).

Los modelos de distribución potencial (MDP) se han utilizado para estimar las distribuciones potenciales de las especies en escenarios actuales y del Cuaternario Tardío (Collevatti et al., 2013; Nogués-Bravo, 2009; Maguire et al., 2015; Peterson & Lieberman, 2012; Waltari et al., 2007). Los MDP correlacionan la presencia de una especie con variables escenopoéticas (por ejemplo, precipitación, temperatura) para identificar regiones en el espacio ambiental que son similares en el espacio geográfico (Guisan & Thuiller, 2005), para reflejar el nicho realizado de la especie (es decir, la suma de todas las condiciones ambientales mínimas necesarias para permitir la persistencia y reproducción de una especie)

y permitir su proyección al espacio o tiempo de interés al investigador. Un método recomendado para probar la precisión de los modelos de paleodistribución (es decir, MDP proyectados a escenarios pasados) es incorporar datos paleontológicos (Maguire et al., 2015; Myers et al., 2015; Nogués-Bravo, 2009), ya que los datos tangibles externos como los fósiles, son evidencia física de procesos biológicos pasados (Maguire et al., 2015; Nogués-Bravo, 2009; Varela et al., 2011), lo que permite validar las hipótesis de distribución utilizando evidencia empírica. Sin embargo, los datos paleontológicos son muy escasos debido a su naturaleza fragmentada y sesgada (Varela et al., 2011), lo que limita este enfoque. Una alternativa viable para probar las metodologías y complementar los resultados de los MDP es el uso de especies virtuales (EV). Este es una herramienta accesible que nos permite analizar los patrones de distribución de una entidad del cual podemos manipular su relación espacial-ambiental, y la cual carece de sesgos de muestreo (Leroy et al., 2014; Meynard & Kaplan, 2013; Meynard et al., 2019; Miller, 2014; Zurell et al., 2010). De esta forma, se puede identificar errores y sesgos inherentes en los modelos de distribución potencial, al tener una forma de contrastar patrones que sabemos que existen contra la información “real” que ofrecen las simulaciones, lo que podría facilitar generar hipótesis realistas biológicamente (Leroy et al., 2014; Meynard & Kaplan, 2013; Meynard et al., 2019).

Los estudios que implementan EV se han enfocado principalmente en explorar varios aspectos metodológicos de los MDP, desde los efectos de la forma y complejidad de respuestas funcionales (García-Callejas & Araújo, 2016; Hirzel & Guisan, 2002), efectos de la resolución o escala del paisaje (Connor et al., 2018), efectos de prevalencia de especies (Fukuda & De Baets, 2016), o efectos de tamaño o estrategias de muestreo (Hallman & Robinson, 2019). Sin embargo, dado que el concepto de nicho ecológico de Grinnell sirve como base para comprender los factores ambientales que influyen en la distribución de las especies (Peterson et al., 2011), las EV también pueden servir como proxy del rango de distribución teórico o esperado de una especie hipotética, ya que sus respuestas ambientales pueden ser delimitados por el programador (Leroy et al., 2016; Meynard et al., 2019). En este sentido, este uso no ha sido plenamente explotado.

En este trabajo evaluamos los cambios potenciales en la distribución histórica y los nichos ecológicos de algunas aves endémicas a bosques secos mesoamericano, comparándolo con los nichos ambientales teóricos proporcionados por EV. Para ello, analizamos seis especies de aves y simulamos EV con diferentes patrones de distribución (endémica de PY, endémica de VPM y disjunta en ambas áreas) bajo tres escenarios temporales del Cuaternario Tardío. En este trabajo se: 1) estimaron la distribución potencial pasada y el solapamiento de nicho entre cada especie de ave y su equivalente distribucional virtual; 2) se probó la hipótesis de conservadurismo/divergencia de nicho entre los parches de bosques secos mesoamericanos representados por las EV; y 3) se evaluó la similitud del nicho ambiental entre cada especie de ave y su contraparte distribucional virtual. Con base en la hipótesis de conservadurismo de nicho (Peterson, 2011; Peterson et al., 1999;), asumimos que los modelos de las EV representan la distribución esperada de una especie hipotética endémica de cada uno de los parches de bosques secos mesoamericanos; por lo tanto, se espera que los modelos de especies de aves y EV puedan predecir distribuciones geográficas potenciales similares (Brown & Carnaval, 2019; Wiens, 2011; Wiens & Graham, 2005). Además, debido a que asumimos un alto grado de conservadurismo de nicho para las EV (Graham et al., 2004; Wiens, 2011; Wiens & Graham, 2005) y su simulación se basó en la extensión total de cada parche de bosque seco mesoamericano, estas especies pueden representar la distribución del propio bioma (Woodward et al., 2004). Por lo tanto, probamos si a) se espera que las especies endémicas de la PY y extendidas (PY-VPM) muestren conservadurismo de nicho, y b) se espera que las especies anteriormente extendidas en el VPM, pero extintas en la PY en la actualidad no muestren conservadurismo de nicho en comparación con otro taxón.

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The role of ecological niche conservatism in the evolution of bird distributional patterns in Mesoamerican seasonally dry tropical forests

ORIGINAL ARTICLE

THE ROLE OF ECOLOGICAL NICHE CONSERVATISM IN THE EVOLUTION OF BIRD DISTRIBUTIONAL PATTERNS IN MESOAMERICAN SEASONALLY DRY TROPICAL FORESTS

Running title: Bird distributional patterns in Mesoamerica

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ABSTRACT

Aim. Due to its complex biogeographical and ecological history, the seasonally dry tropical forests (SDTF) of Mesoamerica are considered a biodiversity hotspot. SDTF are currently distributed in relatively large and continuous, but isolated areas, in which both high total and endemic species numbers. Among birds, few species are shared across SDTF patches; other species are endemic to one of these; and for two species currently endemic to one patch, fossils have been recovered in a different one, suggesting a former widespread distributional pattern in more species, implying that current distributional patterns are probably recent.

Location. Seasonally dry tropical forests of Mesoamerica

Methods. We assessed the role of niche divergence/conservatism in the evolution of bird distributional patterns. Using an ecological niche modelling approach, we estimated paleodistributions for two species currently endemic to the SDTF of Yucatan Peninsula (YP), two to the Mesoamerican Pacific Slope (MPS) with fossil record in the YP, and two more showing an allopatric pattern. For comparison, we simulated virtual species (VS) matching each pattern, assuming they represent the expected distribution of species in each SDTF patch. To test the hypothesis of niche conservatism, we assessed the niche equivalence/similarity between the patches represented by the VS, and in each bird species and its VS distributional counterpart.

Results. Our results showed three main patterns: *i*) no past geographical connectiveness among suitable areas; *ii*) niche conservatism, but not equivalence, despite low niche overlap and geographic distance; and *iii*) potential niche divergence.

Main conclusions. For birds currently endemic to the MPS, our results suggest that absence from the YP may be attributed to the loss of their environmental niche; widespread species showed either niche conservatism or divergence, while endemics showed niche divergence. Our results underline the role of niches divergence/conservatism in the evolution of distributional patterns in the Mesoamerican SDTF avifauna.

KEYWORDS

Distributional changes, distributional patterns, ecological niche evolution, ecological niche modelling, paleodistribution

INTRODUCTION

The Pleistocene period was characterized by a global cooling with a drastic drop in sea levels during glacial periods (Avice & Walker, 1998; Hewitt, 2004; Ramírez-Barahona & Eguiarte, 2013), and warmer interglacial periods that melted the massive ice sheets mainly concentrated in northern latitudes, leading to sea level rise (Hubbard, 1974; Avice & Walker, 1998; Barnosky et al., 2004; Hewitt, 2004; Stewart et al., 2009; Dutton & Lambeck, 2012; Nakazawa & Peterson, 2015; Peterson & Lieberman, 2012). These climatic fluctuations had a major influence on Neotropical biodiversity, promoting changes in demographic dynamics and genetic patterns of species, which consequently modified species distributional patterns (Prance, 1982; Bradbury, 1997; Moritz et al., 2000; Colinvaux & De Oliveira, 2001; Hewitt, 2004; Ramírez-Barahona & Eguiarte, 2013). During glacial periods, forest adapted species responded to these climatic changes either by contracting their ranges into climatically stable areas (historical areas allowing persistence of species during glacial periods), following their environmental preferences through geographic space via niche tracking, therefore retaining similar ecological traits over time (i.e., niche conservatism); by adapting to the new imposing environmental conditions in situ (niche evolution); or underwent extinction if they failed to adapt to novel conditions or disperse to new areas (Wiens & Graham, 2005; Kozak & Wiens, 2006; Peterson et al., 2011; Wiens, 2011).

The origin and historical distribution of seasonally dry tropical forests (hereafter SDTF) has been widely debated (Pennington et al., 2000; Linares-Palomino et al., 2011; Werneck et al., 2011; Collevatti et al., 2013; Banda et al., 2016; Capurucho et al., 2020; Corbett et al., 2020). Regarding to the Mesoamerican SDTF, it has been suggested that a formerly widespread distribution connected the current discontinuous patches during the arid and dry periods of glacial-interglacial cycles (Hubbard, 1974; Metcalfe et al., 2000; Ruiz-Sanchez et al., 2012; Contreras-Negrete et al., 2021). If these patches were ever connected, a high similarity in faunal and floristic composition would be expected. However, high

dissimilarities in species composition in current SDTF patches and across the Neotropics (Herzog & Kessler, 2002; Becerra, 2005; Ríos-Muñoz & Navarro-Sigüenza, 2012; Banda et al., 2016; Oswald et al., 2017; Montaña-Arias et al., 2018; Prieto-Torres et al., 2019a) suggest that independent processes have shaped species composition and diversification patterns, despite apparent habitat continuity (Pennington et al., 2000; Linares-Palomino et al., 2011; Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres et al., 2019a; 2019b; Sánchez-González et al., 2021). This implies a complex evolution for both ecological niches and geographical distributions, which remains poorly understood and only explored in a few taxa (Castillo-Chora et al., 2021a; Hernández-Canchola & León-Paniagua, 2017; Suárez-Mota & Villaseñor, 2020; Sánchez-González et al., 2021).

For endemic birds to Mesoamerican SDTF, concordant biogeographical patterns between phylogenetically distant taxa have been identified; however, biotic composition of these patterns has been assembled via different biogeographical and ecological processes (Herzog & Kessler, 2002; García-Trejo & Navarro-Sigüenza, 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012; Oswald et al., 2017; Prieto-Torres et al., 2019a). Different episodes of avian lineage divergence during the Last Glacial Maximum (LGM ~22-21 kya) suggest that the currently continuous SDTF along the Pacific slope has been periodically interrupted due to phases of isolation, in which environmental conditions may have persisted in climatically stable areas, which may have allowed genetic divergence and persistence of different taxa during glacial periods (Arbeláez-Cortés & Navarro-Sigüenza, 2013; Arbeláez-Cortés et al., 2014; Corbett et al., 2020; Castillo-Chora et al., 2021a; Sánchez-González et al., 2021; Vázquez-López et al., 2021). For bird species in the presently isolated SDTF of the Yucatan Peninsula (hereafter YP), climatic changes from the last glacial-interglacial cycles promoted range fragmentation, which led to environmental isolation and eventual genetic divergence from closely related taxa with different biogeographic affinities (Barker, 2004; Licona-Vera & Ornelas, 2014; Williford et al., 2016; Smith et al., 2018; Vázquez-López et al., 2021). However, although genetic and biogeographic patterns have been relatively well-described, very few studies have focused on the evolution of ecological niches through discerning biotic and abiotic drivers in the evolution and maintenance of species' distributional patterns.

There is evidence that bird species in the Mesoamerican SDTF may have modified their distributional range. Chan (2018) studied Late Pleistocene bird fossils from Loltún Cave in the YP, and assigned some of the identified remains to species currently endemic to the SDTF of the Mesoamerican Pacific slope (hereafter MPS). While this finding cannot be considered as conclusive evidence of a historical connection of currently isolated Mesoamerican SDTF (see Collevatti et al., 2013), it does suggest a past widespread distribution (Hubbard, 1974) in these taxa, as well as a likely dynamic geographical distribution and ecological niche evolution, as previously described for plants (Pennington et al., 2000, 2009). Therefore, studying these past dynamics can improve our understand of the biodiversity patterns of taxa associated with Mesoamerican SDTF (García-Trejo & Navarro-Sigüenza, 2004; Becerra, 2005; Banda et al., 2016; Prieto-Torres et al., 2019a; 2019b).

Species distribution models (SDMs) have been used to estimate species' potential distributions in both present and Late Quaternary scenarios, as these niche-based models allow the analyses of environmental changes influencing range persistence, extension, extinction, or shift (Waltari et al., 2007; Nogués-Bravo, 2009; Peterson & Lieberman, 2012; Collevatti et al., 2013; Maguire et al., 2015). These models use statistical methods to relate geo-referenced localities representing the presence of a species and scenopoetic variables (e.g., precipitation, temperature) to project Grinnellian niches (i.e., the sum of all the minimum environmental conditions necessary to allow the persistence and reproduction of a species; Rödder & Engler, 2011) forecasting suitable areas for a species' presence in the geographical space (Guisan & Thuiller, 2005). This geographical-environmental relationship can be hindcasted to assess suitable areas in past scenarios, known as paleodistribution (Maguire et al., 2015; Nogués-Bravo, 2009; Waltari et al., 2007). This information can be used to test biogeographical hypotheses such as dispersal, historical distribution changes, and niche evolution under climate variations (Peterson et al., 2011).

A recommended method to test the accuracy of paleodistribution models is to incorporate paleontological data (Nogués-Bravo, 2009; Maguire et al., 2015; Myers et al., 2015), since external tangible data such as fossils, are physical evidence of past biological processes (Nogués-Bravo, 2009; Varela et al., 2011; Maguire et al., 2015), therefore allowing validation of the potential distribution hypotheses using empirical evidence. However,

paleontological data is scarcely available due to its fragmented and biased nature (Varela et al., 2011), limiting this promising integrative approach. An alternative to test these models and its performance is the simulation of virtual species (hereafter VS; Miller, 2014; Zurell et al., 2010; Meynard et al., 2019). VS simulate a species' probability of occurrence by defining its environmental suitability and projecting it into a real or simulated landscape (Leroy et al., 2014; Meynard et al., 2019). A virtue of this approach is the control it offers to the user, from defining environmental niche tolerances of the artificial entity to its sampling strategies (Meynard & Kaplan, 2013; Leroy et al., 2014; Meynard et al., 2019). Thus, spatially simulated data represent a "true" species distribution that can be used to identify biases or errors when compared to a real species model (Zurell et al., 2010; Miller, 2014). Studies implementing VS have been mostly focused on exploring various aspects of the SDM framework, from the effects of shape and complexity of functional responses (Hirzel & Guisan, 2002; García-Callejas & Araújo, 2016;), effects of resolution or scale of the landscape (Connor et al., 2018), species prevalence (Fukuda & De Baets, 2016), or effects of sampling sizes or strategies (Hallman & Robinson, 2019). However, since the Grinnellian ecological niche concept serves as a foundation to understand the environmental drivers of species distributional patterns (Peterson et al., 2011), VS can also serve as proxy of a theoretical or expected distributional range, as their environmental responses can be clearly delimited by the programmer (Leroy et al., 2016; Meynard et al., 2019). In this regard, this use has not been fully exploited.

Here we assessed the potential changes in the historical distribution and ecological niches of endemic Mesoamerican SDTF birds by comparison with the expected geographical and environmental niches provided by VS. We analyzed six bird species and simulated VS with different distribution patterns (endemic to YP, endemic to the MPS, and disjunct in both areas) under three Late Quaternary scenarios. Specifically, we: 1) estimated their past potential distribution and the degree of niche overlap between each bird species–VS equivalent; 2) tested the hypothesis of niche conservatism/divergence between the Mesoamerican SDTF patches represented by the VS; and 3) assessed environmental niche similarity between each bird species and their VS distributional counterpart. Based on niche conservatism assumptions (Peterson et al., 1999; Peterson, 2011), we assume that VS models represent the expected distribution of a hypothetical species endemic to each of the

Mesoamerican SDTF patches; therefore, models of bird species and VS are expected to predict similar potential distributional ranges (Brown & Carnaval, 2019; Wiens, 2011; Wiens & Graham, 2005). Also, because we assumed high degree of niche conservatism in the VS (Graham et al., 2004; Wiens, 2011; Wiens & Graham, 2005) and their simulation were based on the whole extent for each Mesoamerican SDTF patches (Woodward et al., 2004), these species may represent the distribution of the SDTF biome itself. Thus, given that niche conservatism is expected to be long term stable on species' geographic distribution (Peterson, 2011; Peterson et al., 2011), we tested whether: a) endemic YP and widespread (YP-MPS) species are expected to show niche conservatism, and b) formerly widespread species (extinct in the YP but present in the MPS), are expected to show no niche conservatism.

MATERIALS AND METHODS

Species selection

We selected six phylogenetically distantly-related resident bird taxa endemic to Mesoamerican SDTF. Given our focus on current patterns in geographic distribution and their possible changes due to Late Quaternary climatic fluctuations, the selected species fulfilled three geographical patterns (Fig. 1):

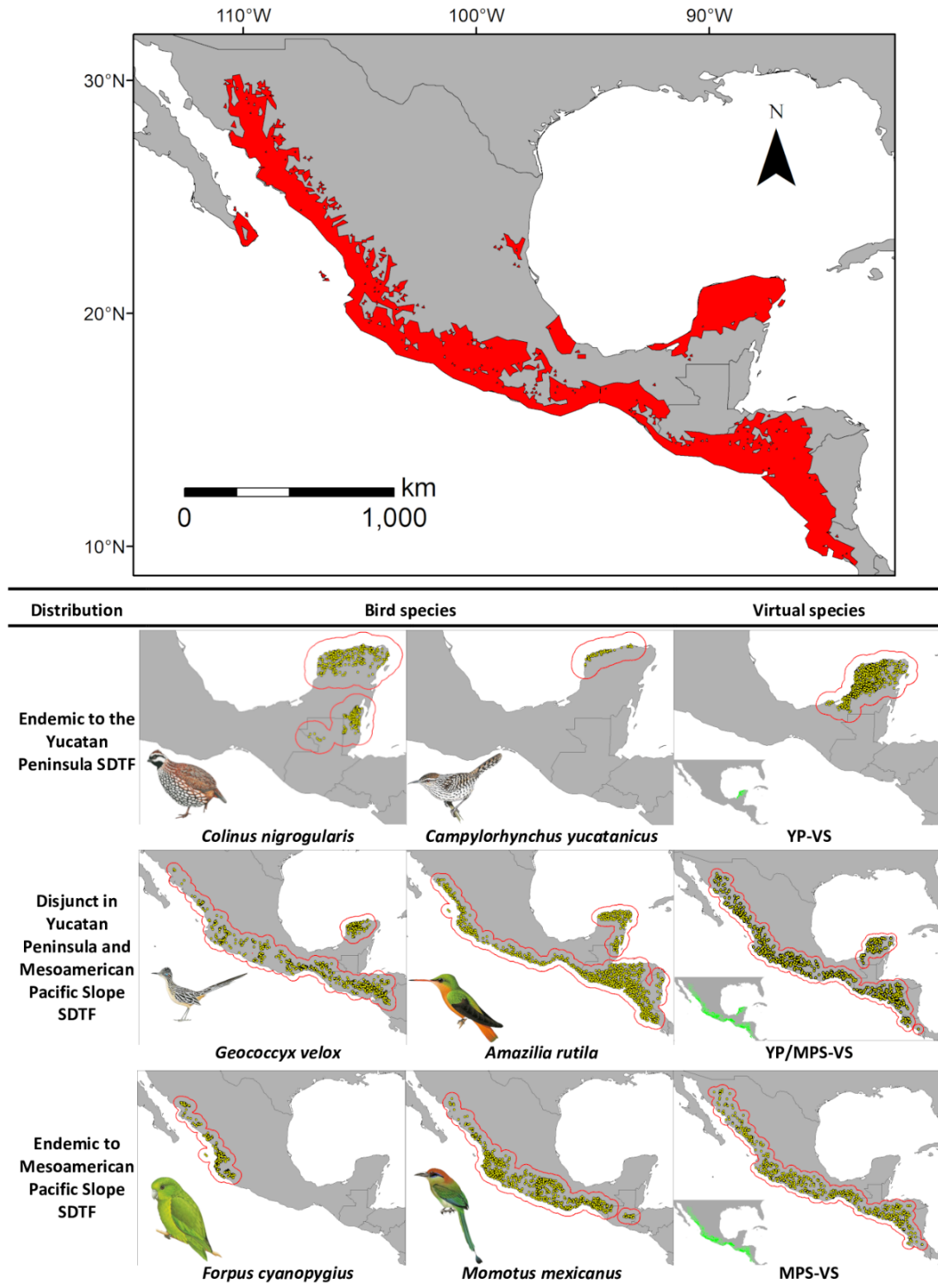


Figure 1. Geographical extent of Mesoamerican seasonally dry tropical forests (above), and the patterns of geographic distribution of the selected species and its virtual species distributional equivalent (below). Occurrence points are denoted in yellow and the accessibility area for each species is delimited in red.

- a) Endemic or quasi-endemic species to the Yucatan Peninsula SDTF (YP SDTF): the black-throated bobwhite (*Colinus nigrogularis*: Odontophoridae) and the Yucatan Wren (*Campylorhynchus yucatanicus*: Troglodytidae);
- b) species with disjunct distribution on the Mesoamerican Pacific Slope SDTF (MPS SDTF) and the YP SDTF: the lesser roadrunner (*Geococcyx velox*: Cuculidae) and the cinnamon hummingbird (*Amazilia rutila*: Trochilidae); and,
- c) current endemic species to the MPS SDTF with fossil record in YP (Chan, 2018): the Mexican parrotlet (*Forpus cyanopygius*: Psittacidae) and the russet-crowned motmot (*Momotus mexicanus*: Momotidae). It is important to note that these fossil remains are not accurately dated yet. However, according to their temporal correlation with the stratigraphic layers, they were collected from deposits corresponding to the Late Pleistocene-Holocene boundary (11.5–9.5 kya). We assume that populations of those species were present in the YP before that interval.

Paleodistribution modelling

To estimate the past potential distributions of the selected species under Late Quaternary scenarios, we used a SDM approach to assess environmental suitability during the present time and to transfer that to the Last Interglacial (LIG, 120 kya), Last Glacial Maximum (LGM, 21 kya) and Mid Holocene (MH, 6 kya) scenarios. Occurrence data for each species were downloaded from the Global Biodiversity Information Facility (GBIF), accessed from Rstudio via the “rgbif” package (<https://cran.r-project.org/web/packages/rgbif/index.html>). We eliminated dubious records and data without spatial information, as well as repeated records from within a radius of 10 km to reduce effects of sampling clustering (Boria et al., 2014). In addition, we performed an environmental filtering by extracting the background values of all 19 bioclimatic variables from each occurrence point and discarded those points without values, as well as outlier records (e.g., Prieto-Torres et al., 2020; Robertson et al., 2016). To delimit the accessibility area (or *M sensu* Soberón & Peterson, 2005), we used a buffer polygon of 75 km around each species occurrence points (e.g., Vázquez-López et al.,

2021). We assumed that M represents both the species' tolerance limits as well as historical/ecological barriers to dispersal across the region (Peterson et al., 2011).

For model building, we used bioclimatic variables for current, LGM, MH and LIG scenarios obtained from WorldClim version 1.4 (available at <https://www.worldclim.org>; Hijmans et al., 2005) at a spatial resolution of 2.5 min (~ 5 km²). Selection of environmental variables for each species was based on a Pearson's correlation test ($r < 0.8$) and variance inflation factor (VIF < 10) from the values extracted from each species occurrence points, using the "corrplot" (Wei & Simko, 2017) and "usdm" (Naimi, 2015) R packages; this step allowed us to ensure that only uncorrelated variables were used. Detailed information about the set of environmental variables used for each species is showed in Supporting information Table S1. We used three general circulation models to predict potential distributions under Late Quaternary: CCSM (Collins et al., 2006), MIROC-ESM (Watanabe et al., 2011) and MPI-ESM-P (Baehr et al., 2015).

The occurrence database for each species was randomly divided in two sets. The first set destined 25% of occurrences data to test the model, and the remaining 75% were used to train the model. We used the "kuenm" R package (Cobos et al., 2018) which is based on MaxEnt (v. 3.4.4) algorithm (Phillips et al., 2006), for model calibration, building, evaluation, and extrapolation analysis. All 31 combinations of MaxEnt features classes (linear, quadratic, product, threshold, and hinge), 18 regularization multiplier values (0.4 to 2 at intervals of 0.2, 2 to 6 at intervals of 0.5 and 8) and a single set of climatic non-correlated variables were used for model calibration for each species. Model selection was based on statistical significance, omission rate, and complexity. Thus, every candidate model per species was evaluated, and the best model was selected based on: a) statistical significance according to the Area under the curve (AUC) ratio ≤ 1 , with 500 iterations, 50% of data for bootstrapping and cloglog output (Phillips et al., 2017); b) data omission rate (how well the models created with training data predict the test data occurrences) $\leq 5\%$; and c) Akaike information criterion corrected for small samples (AICc) ≤ 2 . Final models selected by these criteria were replicated ten times, and we considered the median of these replicates as the best estimate (Campbell et al., 2015). When more than one final model was retained, we selected the most parsimonious (i.e., with the least number of parameters; Daganzo et al.,

2012). We also used two methods of extrapolation: unconstrained extrapolation and no extrapolation.

Then, we considered the threshold corresponding to the 10th percentile of training presence to binarize the suitability values outputs. In addition, we performed a mobility-oriented parity test (MOP test) to quantify model uncertainty associated to extrapolation (e.g., estimation of areas in which environmental conditions are outside the range of conditions contained in the calibration area; Elith et al., 2010), as non-analogous climatic conditions may lead to misinterpretations of the models (Owens et al., 2013; Alkische et al., 2017). We inspected visually the models obtained with both forms of extrapolation for each species and discarded those with little ecological or biological realism (e.g., suitability estimation in highlands, over or underprediction, predictions in areas of high environmental extrapolation, ecologically unfeasible response curves). Finally, we created a consensus map based on common areas estimated from all three general circulation models for each temporal scenario.

Virtual species simulation and modelling

We generated three VS using the "virtualespecies" R package (Leroy et al., 2016) matching the distribution range of our selected bird species. Therefore, VS simulated species included endemic species to the YP SDTF, endemics to MPS SDTF, and a species with disjunct distribution in both areas. We followed Santini et al., (2021) to generate VS in which the user determines a specific climatic niche tolerance before projecting it into the geographic space (Leroy et al., 2016; Meynard et al., 2019). Using current climatic conditions allowed us to have a criterion to determine niche tolerance values, as well as having a greater control over the geographic distribution of the VS. The climatic niche values used to define the VS niche tolerance were based on current climatic conditions of the Mesoamerican SDTF (Fig. 2).

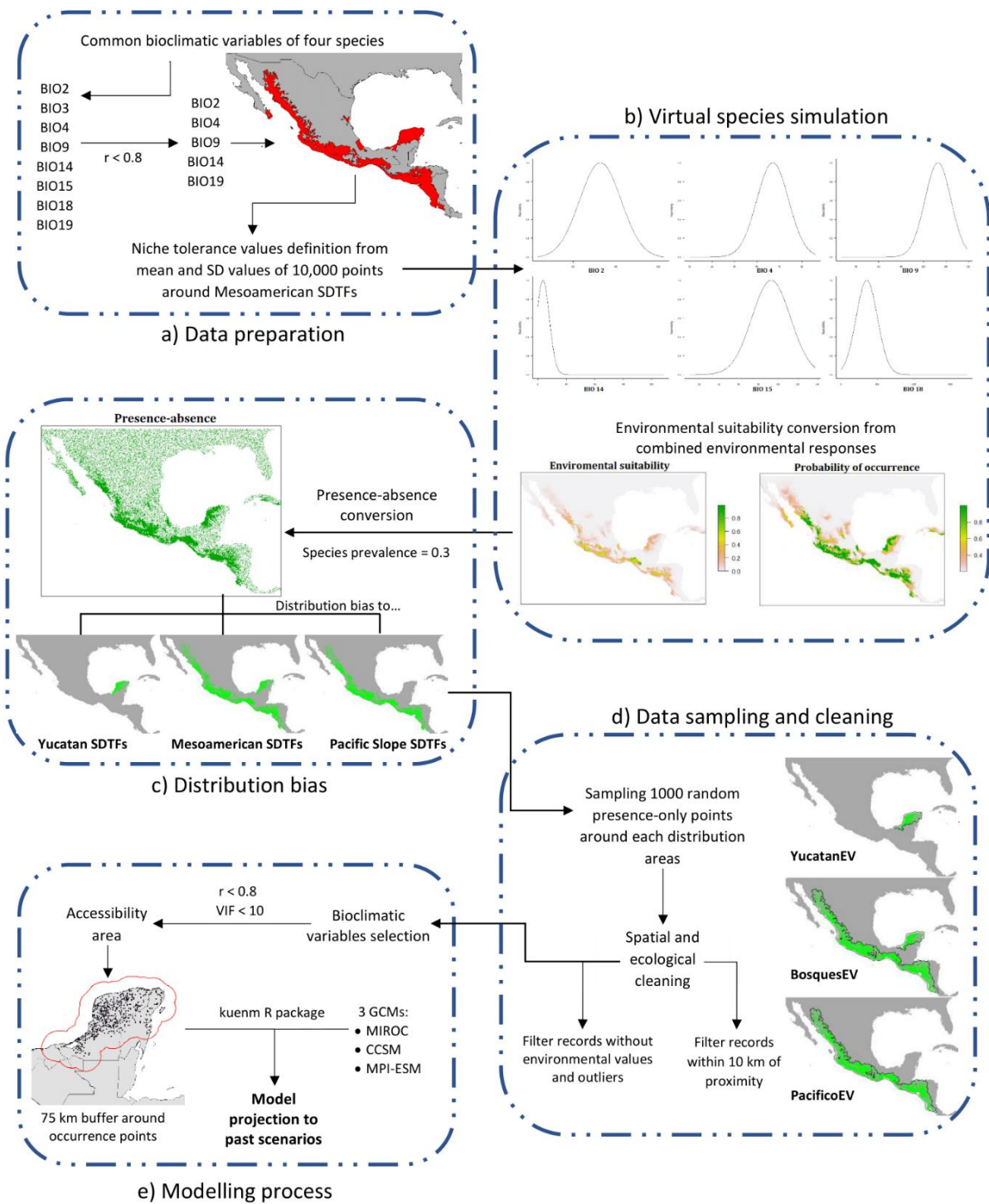


Figure 2. General workflow of the steps taken on virtual species generation, data sampling and its ecological modelling.

To select the bioclimatic variables for the VS simulation, we performed a correlation test using common bioclimatic variables for four of the six study species (BIO 2, BIO 3, BIO 9, BIO 14, BIO 15, BIO 18, BIO 19) using the “removeCollinearity” function of the “virtualspecies” package and discarded those with correlation higher than 80% ($r > 0.8$). Then, to determine the climatic niche tolerances of the VS, we sampled environmental values of the non-correlated variables within the study area using 10,000 random points and calculated their mean and standard deviation (Santini et al., 2021). The environmental responses for each variable were defined as fit to a normal distribution and were combined multiplicatively to create a unique environmental suitability relation (Leroy et al., 2016). To estimate the probability of presence of the VS throughout its distribution range, we converted the environmental suitability to a presence-absence pattern using a logistic conversion. In this way, probability of presence for each pixel is estimated according to its environmental suitability value (Leroy et al., 2016). Species prevalence (i.e., the number of pixels occupied by the species out of the total pixels available) was set at 0.3, following published recommendations for creating an accurate and unbiased model (McPherson et al., 2004; Liu et al.; 2005; Santika, 2011; Hanberry & He, 2013; Guo et al., 2015; Sor et al., 2017).

We then introduced a distribution bias to assess three scenarios of geographic distribution, simulating three species in non-equilibrium (i.e., not present in all climatically suitable areas; Araújo, 2005; Svenning & Skov, 2007; Nogués-Bravo, 2009) with the environment. We restricted the distribution of the VS to different Mesoamerican SDTF patches in order to simulate three species endemics to each patch: “YP-VS”, “YP/MPS-VS” and “MPS-VS”. We used a polygon with an added 10 km buffer around each SDTF patch and sampled 1000 random presence-only points within each patch. The dataset for each VS was spatially and environmentally cleaned, eliminating records within 5 km of proximity, outliers, and records without environmental values (Supporting Information 3).

Environmental variables selection, definition of accessibility area for each generated VS and their paleodistribution modelling, all followed the same procedure as for the bird species (i.e., variables selected with Pearson correlation [$r < 0.8$] and VIF [< 10]; a M delimited with a buffer polygon of 75 km around the occurrence points, and both the same circulation models and projections to past scenarios). We employed the same parameters as

in the bird species (31 features combinations, 18 regularization multipliers and a single set of bioclimatic variables) for model calibration, creation and evaluation using the “kuenm” package (Cobos et al., 2018). Then, we followed the same procedures as the bird species for the model calibration, model selection, and binary map conversion in the current and past climate scenarios (based on the three general circulation models).

Background similarity and ecological niche overlap analyses

We assessed the degree of geographical matching between the bird species and its VS distributional equivalent by overlapping the corresponding binary maps obtained for each temporal scenario. This procedure allowed us to assess common areas of climatic stability between each bird species-VS distributional equivalent over time. We employed the PCA-env method (Broennimann et al., 2012) to test the hypothesis of niche conservatism between the Mesoamerican SDTF patches via the estimation of the ecological niche overlap represented by the VS. Then, to assess the role of abiotic drivers in the distribution of birds endemic to Mesoamerican SDTF, we estimated the degree of niche overlap between each bird species –VS distributional equivalent.

First, we used a principal component analysis (PCA) to transform the common bioclimatic variables for each of the pairwise bird species-VS distributional equivalent comparison into a two-dimensional space defined by the first and second principal components (Jolliffe & Cadima, 2016). Then, we used a niche equivalency and background similarity tests to evaluate the observed similarity between each pairwise comparison. The niche equivalency measures the identity or equivalency of two species environmental niches by applying a Monte Carlo resampling for a given number of iterations (Warren et al., 2008; Broennimann et al., 2012; Brown & Carnaval, 2019). On the other hand, the background similarity evaluates the niche similarity in each pairwise comparison by applying a spatial randomization of occurrences of a species within the accessible area of the other species and vice versa, and then calculates the overlap between them for a given number of iterations (Broennimann et al., 2012; Brown & Carnaval, 2019). In both tests, a *Schoener's D* and *Hellinger's I* similarity measure indexes ranging from 0 (no niche overlap) to 1 (complete niche overlap) are generated. Null hypothesis of niche equivalency (bird and virtual species

exhibit identical environmental preferences) and background similarity (differences in environmental preferences are due to differences in climate availability) between each VS and bird species-VS pairwise comparisons are accepted only if the observed *D* value is significantly higher ($P < 0.05$) than values expected from 1,000 pseudo-replicated data sets allowing random shifts. All these procedures were done using “ecospat” (Di Cola et al., 2017) and “humboldt” (Brown & Carnaval, 2019) R packages.

RESULTS

Paleodistribution modelling and virtual species

We obtained 10,380 occurrence data for *C. nigrogularis*; 3,947 for *C. yucatanicus*; 9,124 for *G. velox*; 129,125 for *A. rutila*; 1,563 for *F. cyanopygius*; and 22,089 for *M. mexicanus*. After spatial and environmental filtering, 52 occurrence points were retained for *C. yucatanicus*, 486 for *C. nigrogularis*, 735 for *G. velox*, 1485 for *A. rutila*, 243 for *F. cyanopygius*, and 780 for *M. mexicanus*. As for the VS, from 1000 random points sampled within each region, 346 occurrence points were retained after spatial and environmental cleaning for YP-VS, 449 for YP/MPS-VS and 411 for MPS-VS.

A total of 589 candidate models per species were generated as the result of calibration process. Each of these models was evaluated and the best models were selected based on statistical significance, an omission rate of less than 10%, and the lowest complexity level. All final models yielded a good performance in AUC (> 0.75) and mean AUC values (i.e., ROC-partial) higher than 1 (Table 1), indicating that models performed better than random and are statistically descriptive of the climatic conditions defining the environmental niche of each taxon and VS. According to the Jackknife test and variables contribution percentage (Supporting information 1, Table S1), the most important variables for model building for each species were: Precipitation of Wettest Month (BIO 13) for *C. nigrogularis* (43.2%) and *C. yucatanicus* (58.4%); Mean Diurnal Range (BIO 2) for *G. velox* (33.3%); Isothermality (BIO 3) for *A. rutila* (20.6%); Precipitation of Warmest Quarter (BIO 18) for *F. cyanopygius* (31.4%); and for *M. mexicanus* was Precipitation of Driest Month (BIO 14, 28%). As for the VS, the most important variables were Mean Diurnal Range (BIO 2) for YP-VS (34.7%); Mean Temperature of Driest Quarter (BIO 9) for MPS/YP-VS (22.2%); and Annual Mean

Temperature (BIO 1) for MPS-VS (35.4%). With a VS prevalence value set at 0.3, the value of α (defines the curvature of the environmental suitability curve) was fixed at -0.05 and β (i.e., the inflection point of the curve) was of 0.030 (S3). Thus, the VS is present in 30% of the available geographic areas for each SDTF (or pixels; Leroy et al., 2016). It is important to note that mean MOP analysis suggest a large amount of non-analogous environmental conditions (strict extrapolation areas) as calibrated from the accessibility area for the species endemic to the YP (*C. nigrogularis*, *C. yucatanicus* and YP-VS), as well as for *F. cyanopygius*, mainly in the LIG and LGM periods (Supporting information 2, Fig. S1).

Table 1. Parameters and statistical evaluation of the best model selected for each species. RM= Regularization multiplier; Features: l= linear, p= product, q= quadratic, t= threshold, h= hinge.

| Species | RM | Features | AUC | Mean AUC ratio | Omission rate at 5% | Number of parameters |
|------------------------------------|-----|----------|-------|----------------|---------------------|----------------------|
| <i>Campylorhynchus yucatanicus</i> | 0.6 | lqp | 0.927 | 1.720 | 0.025 | 4 |
| <i>Colinus nigrogularis</i> | 1.6 | lpt | 0.835 | 1.184 | 0.058 | 34 |
| <i>Geococcyx velox</i> | 0.4 | lqp | 0.799 | 1.241 | 0.021 | 32 |
| <i>Amazilia rutila</i> | 0.4 | qp | 0.775 | 1.146 | 0.024 | 29 |
| <i>Forpus cyanopygius</i> | 1.4 | pt | 0.880 | 1.358 | 0.021 | 38 |
| <i>Momotus mexicanus</i> | 0.6 | lqp | 0.785 | 1.117 | 0.023 | 14 |
| Virtual species | RM | Features | AUC | Mean ROC ratio | Omission rate at 5% | Number of parameters |
| YP-VS | 2.5 | qt | 0.831 | 1.421 | 0.050 | 14 |
| YP/MPS-VS | 0.4 | lqp | 0.832 | 1.470 | 0.034 | 34 |
| MPS-VS | 5.5 | pth | 0.836 | 1.440 | 0.022 | 21 |

For endemic species to the YP, models of *C. nigrogularis* (Fig. 3) showed few overlap areas with YP-VS (3.59%). Limited environmental suitable areas were predicted on northwestern YP and in isolated patches on Central America during the LIG and LGM, while the MH scenario mostly resembles its current distribution. Also, suitable areas were predicted in the central MPS in all temporal scenarios. For the *C. yucatanicus* (Fig. 4), models showed the least overlap areas of all pairwise bird-VS distributional equivalent (1.67%). Its potential distribution was predicted in the northern fringe of YP in all past scenarios, similar to its current distribution; however, during the LGM it may have expanded to the northwest, when the YP reached its maximum geographic extension. As for the models of species with disjunct distribution, *G. velox* (Fig. 3) showed higher overlap areas with YP/MPS-VS (18.84%) in

comparison with *A. rutila* (8.02%, Fig. 4) in all temporal scenarios, except in LIG. A major difference between both species models is that *G. velox* predicted more fragmented suitable areas in comparison with *A. rutila*, which appears to be more continuous through its distributional range. However, the LGM projections for both species suggest fragmented and restricted suitable areas along the MPS and a more extensive distributional range in the YP.

Regarding species currently endemic to the MPS SDTF, models of *F. cyanopygius* (Fig. 3) showed fewer overlap areas with its VS distributional equivalent (16.80%) than *M. mexicanus* (63.94%). The models suggest that the YP would have had environmentally suitable conditions for this species during the LIG, retracted southward during the LGM, and expanded out during the MH, while suitable conditions on the MPS would have been restricted to the coasts during the LIG, retracted northward to Nayarit-Jalisco during the LGM and expanded out from it during the MH, achieving its current range. Models for *M. mexicanus* (Fig. 4) showed the most overlap areas of all pairwise bird-VS distributional equivalent (63.94%). Suitable areas in YP were predicted across all time scenarios, albeit restricted to the northwestern fringe of the peninsula during the LIG and LGM, while continuous suitable environmental areas were predicted on the MPS in all time scenarios.

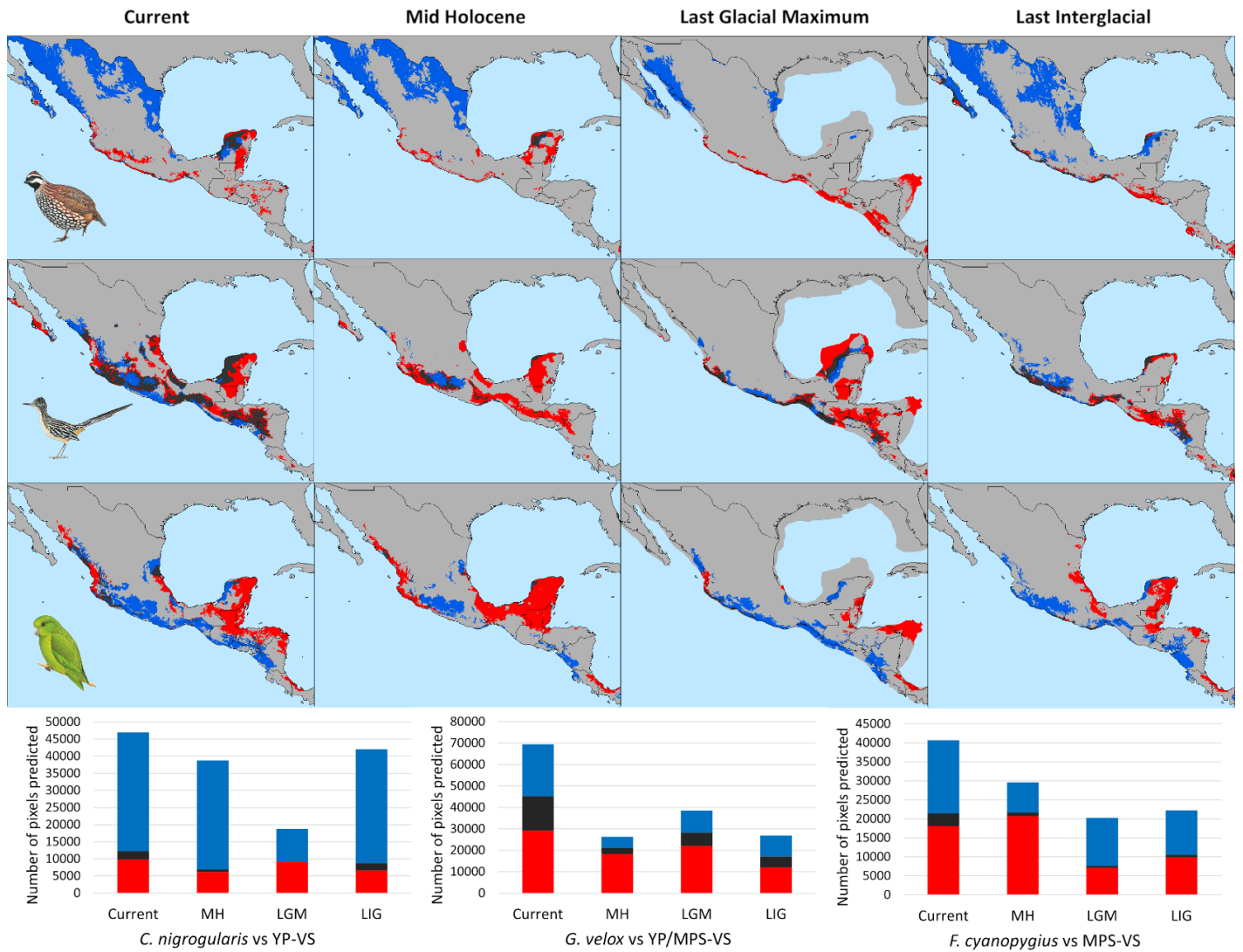


Figure 3. Consensus ecological niche models of *C. nigrogularis*, *G. velox* and *F. cyanopygius* (in red) with their virtual species distributional equivalent (in blue) associated with Mesoamerican SDTF, projected under past temporal scenarios. Overlap areas for both species models are depicted in grey. Graph bars correspond to the number of pixels (size of the area) predicted by models for each species (red), their virtual species equivalent (blue) and both species overlap (grey) across the four-time scenarios.

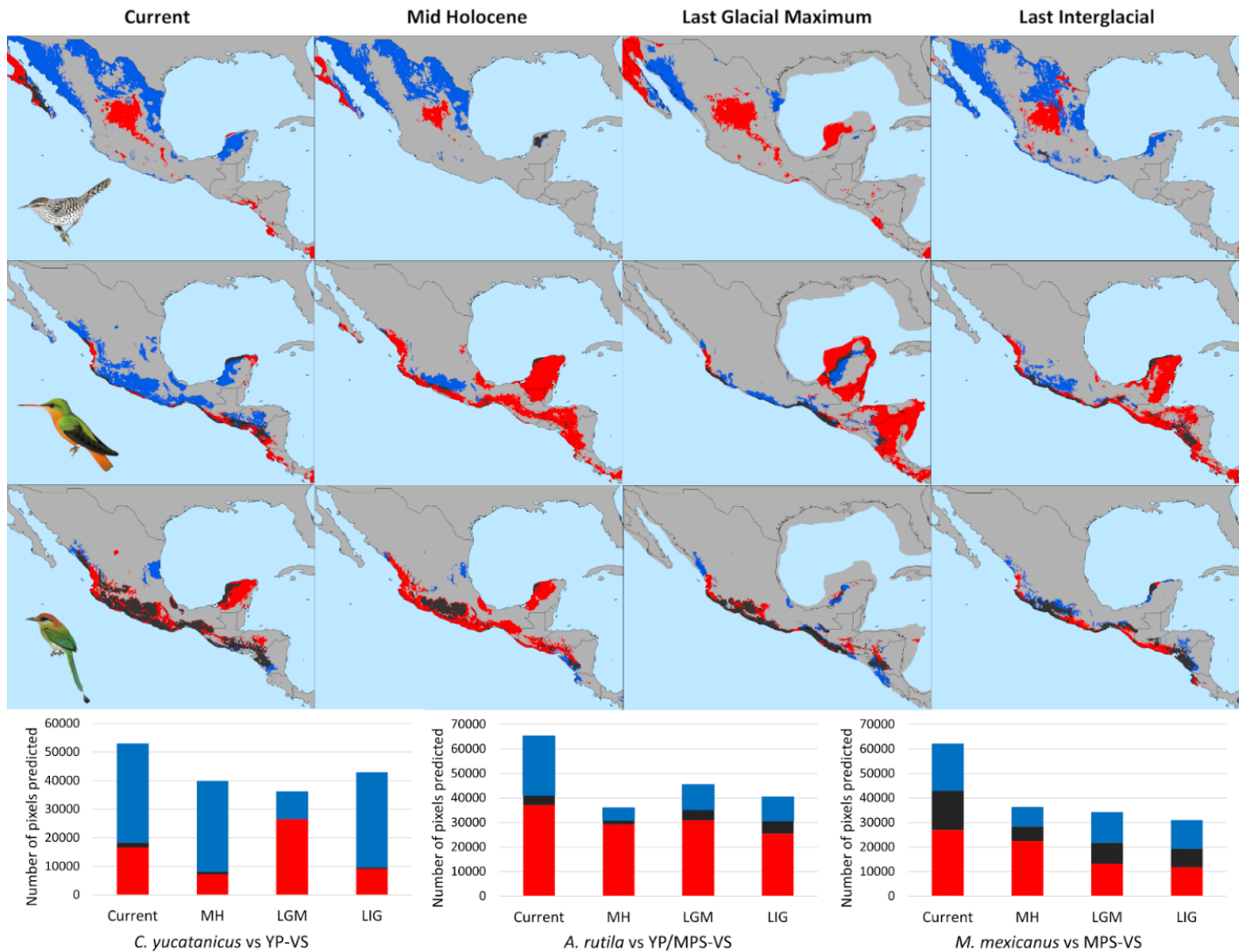


Figure 4. Consensus ecological niche models of *C. yucatanicus*, *A. rutila* and *M. mexicanus* (in red) with their virtual species distributional equivalent (in blue) associated with Mesoamerican SDTF, projected under past temporal scenarios. Overlap areas for both species models are depicted in grey. Graph bars below correspond to the number of pixels (size of the area) predicted by models for each species (red), their virtual species equivalent (blue) and both species overlap (grey) across the four-time scenarios.

Niche conservatism tests

PCA-env of pairwise comparisons among VS indicated that an average of 68.95% of the observed environmental variance is explained by the first two components (PC1 = 46.54% and PC2 = 22.41%). We rejected the null hypothesis of niche equivalency for all niche equivalency tests ($P > 0.05$), which indicate that ecological niches are not statistically identical for all pairwise comparisons between VS (Table 2, Fig. 5). However, our niche

similarity tests showed that for all pairwise comparisons, the observed niche was more similar than expected by chance ($P < 0.05$), therefore suggesting that YP SDTF, MPS SDTF and the disjunct distribution of YP and MPS SDTFs, occupy similar but not equivalent environmental niches.

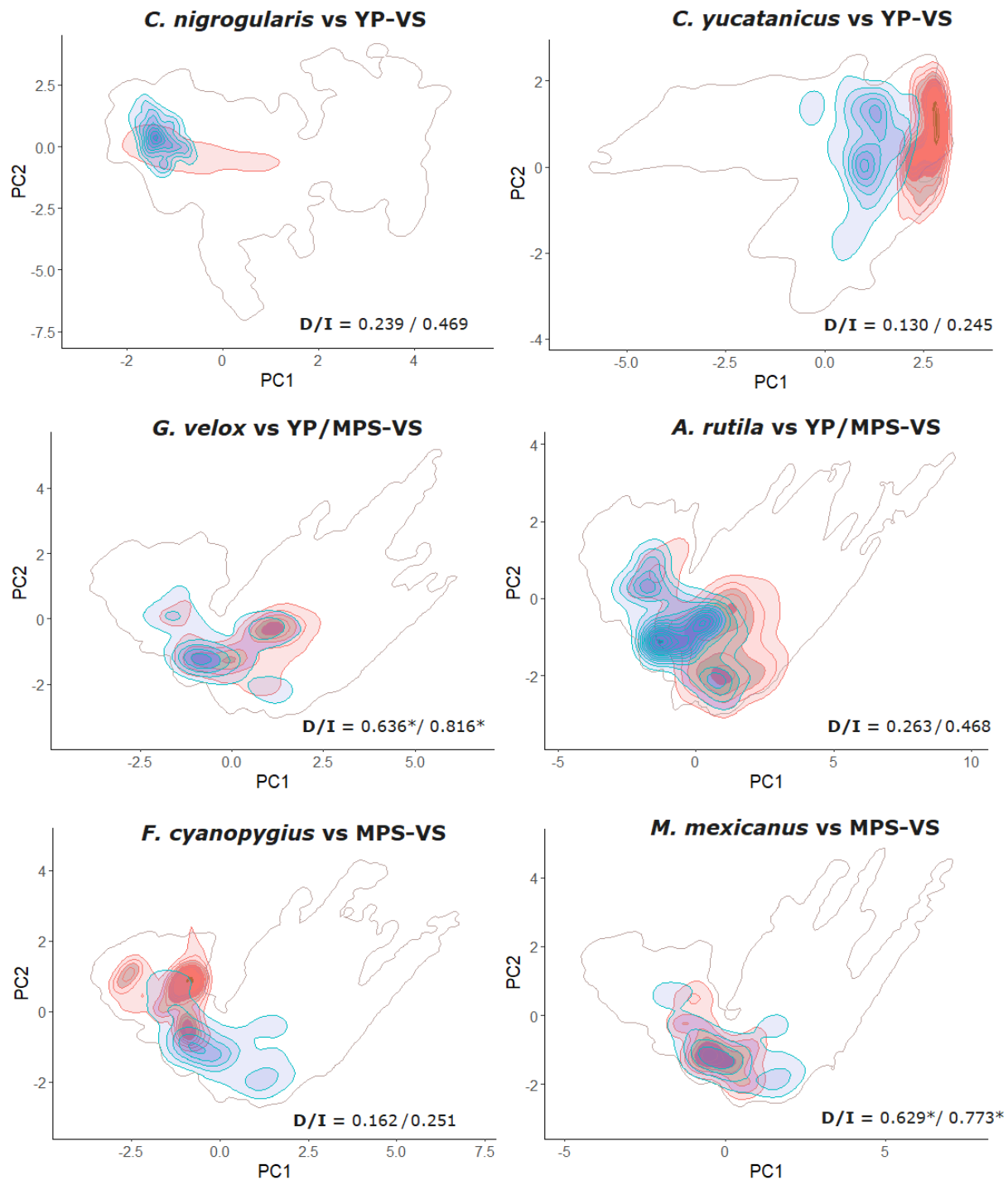


Figure 5. Niche overlap for each of the pairwise comparisons between bird species and its virtual species distributional equivalent associated with different patches of Mesoamerican SDTF. The graphs depict the species niches along the first two axes of the PCA-env. The red lines represent the kernel density isopleths at different densities (from 10 to 100%) of the bird species niche, the blue lines represent the same for the virtual species and the grey contour represents the 1% kernel density of the environmental space boundaries. The *Schoener's D* and *Hellinger's I* similarity indexes are indicated in all plots, with their statistical significance expected from a 1,000 pseudoreplicates (* = significant in both directions).

Table 2. Summary of the results of ecological niche comparisons between the three virtual species. This table lists the variation explained by the first (PC1) and second (PC2) principal components for each pairwise comparison tests, their niche overlap indexes of Schoener's *D* and Hellinger's *I* and the *p* values of the observed *D* index in both directions; VS = virtual species. * indicate statistically significant results ($P < 0.05$).

| Test | | PC1 | PC2 | Niche overlap | | Niche equivalency | Niche similarity (p value) | |
|---------------------|------|--------|--------|---------------|----------|-------------------|----------------------------|--------------|
| VS 1 | VS 2 | | | <i>D</i> | <i>I</i> | | VS 1 vs VS 2 | VS 2 vs VS 1 |
| YP-VS vs MPS-VS | | 50.62% | 21.8% | 0.128 | 0.347 | Different | *0.031 | *0.041 |
| YP-VS vs YP/MPS-VS | | 36.52% | 27.1% | 0.126 | 0.351 | Different | *0.010 | *0.008 |
| YP/MPS-VS vs MPS-VS | | 52.5% | 18.34% | 0.832 | 0.933 | Different | *0.002 | *0.001 |

PCA-env comparisons between bird species and their VS distributional counterpart indicated that an average 72.42% of the environmental variance is explained among groups (PC1 = 51.50% and PC2 = 20.92%). Niche equivalency tests indicated that the environmental niche in all pairwise comparisons between bird and virtual species are not equivalent ($P > 0.05$). However, pairwise comparisons between *G. velox* vs YP/MPS-VS and *M. mexicanus* vs MPS-VS, showed the highest niches overlap values and their niche similarity tests are statistically significant ($P < 0.05$) (Table 3). These results suggest that both species occupy similar environmental niches as their VS distributional counterpart. We rejected the hypothesis of niche similarity for all other pairwise comparisons, as the observed *D* values are statistically non-significant, which suggest that *C. nigrogularis*, *C. yucatanicus*, *A. rutila* and *F. cyanopygius* occupy different environmental niches than their VS distributional counterpart.

Table 3. Summary of the results of ecological niche comparisons between each bird taxa and their virtual species distributional equivalent. This table lists the variation explained by the first (PC1) and second (PC2) principal components for each pairwise comparison tests, their niche overlap indexes of Schoener's D and Hellinger's I and the p values of the observed D index in both directions. BS = bird species; VS = virtual species. *indicate statistically significant results ($P < 0.05$).

| Test | PC1 | PC2 | Niche overlap | | Niche equivalency | Niche similarity (P value) | |
|---------------------------------|--------|--------|---------------|-------|-------------------|----------------------------|----------|
| | | | D | I | | BS vs VS | VS vs BS |
| <i>C. nigrogularis</i> vs YP-VS | 44.77% | 27.84% | 0.239 | 0.469 | Different | 0.119 | 0.109 |
| <i>C. yucatanicus</i> vs YP-VS | 60.32% | 24.31% | 0.130 | 0.245 | Different | 0.323 | 0.329 |
| <i>G. velox</i> vs YP/MPS-VS | 46.17% | 17.53% | 0.636 | 0.816 | Different | 0.018* | 0.021* |
| <i>A. rutila</i> vs YP/MPS-VS | 51.33% | 14.12% | 0.263 | 0.468 | Different | 0.154 | 0.129 |
| <i>F. cyanopygius</i> vs MPS-VS | 53.98% | 18.5% | 0.162 | 0.251 | Different | 0.230 | 0.210 |
| <i>M. mexicanus</i> vs MPS-VS | 52.44% | 23.19% | 0.629 | 0.773 | Different | 0.025* | 0.029* |

Except for *G. velox* and *M. mexicanus*, we found no evidence of niche conservatism in the pairwise comparisons among birds and VS in the selected species (Table 3). Regarding distributional patterns, we found mixed support for widespread (YP and MPS) species: while niche conservatism is suggested for *G. velox*, the contrary was indicated for *A. rutila*. Similarly, for formerly widespread species (currently endemic species to the MPS with Pleistocene fossils in the YP), we found evidence of niche conservatism in *M. mexicanus*, but no for *F. cyanopygius*. For YP endemics, no niche conservatism was indicated in the two studied species.

DISCUSSION

Multiple studies on biotic patterns across the Neotropics have suggested that each main SDTF patch possess a singular evolutionary history, which has promoted high levels of diversity and endemism in different taxa despite environmental similarity (Pennington et al, 2000; Porzecanski & Cracraft, 2005; Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres et al., 2019a; 2019b). A few Mesoamerican SDTF species, however, are widely distributed sharing different patches (Prieto-Torres et al., 2019a; 2019b; Ríos-Muñoz & Navarro-Sigüenza, 2012), suggesting that environmental similarity also allows for the species' persistence, due to niche conservatism, which may be long-term stable in terms of geographic distributions

(Peterson et al., 2011). Given that adaptative processes are suggested to be slower than extinction processes (Holt & Gomulkiewicz, 1996), widely distributed species are expected to show niche conservatism, implying that no conservatism may led either to adapt to suboptimal environments, to evolve responses to novel environmental conditions, or to extinction if species are unable to track proper suitable conditions (Holt, 1990).

Paleodistribution models

Paleodistribution models for both bird and virtual species showed that potential suitable areas would have been disjunct in YP and the MPS SDTF since at least the LIG (120k years), as our findings do not support a recent widespread SDTF on Mesoamerica due to highly limited to no connectiveness, as our models showed. In fact, the MOP analysis showed that most of predicted suitable areas for the YP endemics (*C. nigrogularis*, *C. yucatanicus* and YP-VS) are not environmentally analogous to the calibration area during the LGM. Instead, analogous environmental conditions were highly restricted along the extended, but currently submerged shorelines of eastern Central America (Supporting information 2, Fig. S1). However, high values of extrapolation may be explained, in part, by a mosaic of vegetation held in the YP, not analogous to the present during this time (Cruz et al., 2016), with relatively mesic conditions in the south (Metcalf et al., 2000; Hodell et al., 2008; Bush et al., 2009; Correa-Metrio et al., 2012;), higher precipitation levels in the center of the peninsula (Metcalf et al., 2000; Brenner et al., 2002; Cruz et al., 2016) and differed rainfall patterns (more rain falling during the wet season than during the dry season) in comparison to the present (Hodell et al., 2008). Changes in the extension and geographic distribution of environmental suitable areas (as clearly seen in *C. nigrogularis*) suggest that endemic species may have “tracked” proper environmental conditions allowing their persistence in the region at least in these periods.

For *C. yucatanicus*, more arid and dry conditions in the north during the LGM allowed its expansion to the then emerged area of YP, while the opposite may have occurred for *C. nigrogularis*, when moist forests expanded in response to wet periods around the south and center of the peninsula, restricting its potential distribution (Williford et al., 2016). For both species, fluctuations in rainfall patterns may have influenced their potential distribution

around this period, as they are heavily dependent on precipitation (Supporting information 1, table S1). Increased environmental suitability were predicted after early to mid-Holocene, following the gradual establishment of similar-to-present environmental conditions in the YP (Metcalf et al., 2000; Brenner et al., 2002; Carrillo-Bastos et al., 2010). This result matches with phylogeographic studies of plants (Montalvo-Fernández et al., 2018) and mammals (León-Tapia, 2020) in the region.

Our models for YP-VS seem to support the lack of suitable conditions in past scenarios for endemic species to the YP: a virtual species fine calibrated to current environmental conditions of YP SDTF did not find suitable areas during the LGM in the peninsula, because current analog environmental conditions would be extremely limited, or even non-existent. This suggests that either the range of an endemic species to YP SDTF would be very limited during this period, or perhaps there were no endemic species in these forests. The latter is supported by the fact that, despite high levels of geographic endemism in YP (Paynter, 1955; Cortés-Ramírez et al., 2012), most of the endemic species are not ecologically restricted to dry forests (Paynter, 1955; White & Hood, 2004; Cortés-Ramírez et al., 2012; Prieto-Torres et al., 2019b). This may be explained by the relatively young age of YP SDTF (Becerra, 2005; Vázquez-Domínguez & Arita, 2010), which has not been isolated long enough to allow species differentiation (Cortés-Ramírez et al., 2012). However, recent phylogenetic studies have recognized previously conspecific bird species inhabiting YP SDTF as full species (e.g., *Campylorhynchus yucatanicus*: Barker, 2007; *Polioptila albiventris*: Smith et al., 2018). These speciation events are consistent with episodes of population isolation and gradual climatic divergence (McCormack et al., 2010) due to differences in climatic conditions in the peninsula (Estrada-Loera, 1991), which is supported by our results from niche equivalency and similarity tests. These climatic differences may have promoted genetic divergence on some taxa (e.g., the Mexican sheartail *Doricha eliza*: Licona-Vera & Ornelas, 2014; or the grayish mouse opossum *Tlacuatzin canescens*: Arcangeli et al., 2018), as well as changes on body size in some bird species (Silva-Martínez et al., 2023). Therefore, the restricted suitable areas and non-analog environmental conditions predicted in past scenarios for YP-VS are concordant with these events, underlining the importance of environmental processes in shaping the YP complex biota (Vázquez-Domínguez & Arita, 2009; Duno-de Stefano et al., 2012; Prieto-Torres et al., 2019a, 2019b).

We found less variation in predicted suitable areas for disjunct distributed species and endemic species to the MPS SDTF. Our projection towards the LGM mostly coincide with hypothesized climatically stable areas and phylogeographic breaks zones reported previously in phylogeographic studies of birds inhabiting the MPS (Arbeláez-Cortés et al., 2014; Castillo-Chora et al., 2021a) and plants from the Mexican Tropical dry forests (Becerra & Lawrence, 2008). Climatically stable areas estimated between Nayarit-Jalisco, along the MPS, were also found for *G. velox*, *A. rutila*, *F. cyanopygius* and YP/MPS-VS, and is consistent with other bird species (Castillo-Chora et al., 2021a; 2021b; Vázquez-López et al., 2021), as well as other animals (Demastes et al., 2002; Dewitt et al., 2008). Climatically stable areas predicted for *M. mexicanus* and MPS-VS are consistent with results in Arbeláez-Cortés et al., (2014), who proposed that the marked phylogeographic structure in this species is the result of concordant phylogeographic breaks throughout the Pacific lowlands and indicative of an older date haplogroup differentiation.

Models of YP/MPS-VS and MPS-VS predicted similar suitable areas and showed similar temporal patterns. In particular, the contraction to the Balsas Basin (Flores-Tolentino et al., 2021) during the LIG and MH, and later expansion to a more widespread distribution during the LGM and current time scenarios resembles the Interglacial Refugia Hypothesis, which suggest that species contracted to warm/humid refugia during interglacials and expanded out under the cold/dry climate of the LGM (Contreras-Negrete et al., 2021; Cornejo-Romero et al., 2017). Conversely, the inverse pattern was found for *G. velox*, *A. rutila* and *F. cyanopygius*, which roughly resembles the Glacial Refugia Hypothesis, in which posits that species ranges contracted to different refugia during the cold/dry glacial periods and later expanded following the warm/humid interglacial periods (Avice & Walker, 1998; Hewitt, 2000; Cornejo-Romero et al., 2017). Both patterns describe demographic dynamics of Neotropical dryland plants (Cornejo-Romero et al., 2017; Ornelas et al., 2018; Montalvo-Fernández et al., 2019; Contreras-Negrete et al., 2021).

As for species currently endemic to the MPS SDTF, our models for both species match spatially with the fossil locality on the YP (Chan, 2018), and suggest two patterns of range contraction during the LGM. Considering that the collected fossils correspond to the Pleistocene-Holocene boundary (see methods), their presence on the peninsula predates this

time, as suggested by our LIG and LGM projections. For *F. cyanopygius*, the range contraction in the MPS matched the predicted areas of climatic stability of some endemic birds to the region (Arbeláez-Cortés & Navarro-Sigüenza, 2013; Arbeláez-Cortés et al., 2014; Castillo-Chora et al., 2021a), while the southerly shift for the YP population have also been found for other taxa as well (Castillo-Chora et al., 2021b; Montalvo-Fernández et al., 2019). For *M. mexicanus*, we found widespread climatically stable areas along the MPS (see also Arbeláez-Cortés et al., 2014), while suitable conditions for the YP population, along with MPS-VS, were restricted to the northern and most arid part of the peninsula (Paynter, 1955), which have not been documented previously for paleodistribution studies of YP taxa.

Ecological niche analysis

Our environmental niche tests between the VS suggest that although the environmental niches are not identical or equivalent, their observed niches are more similar than expected by chance, as expected for species with allopatric populations (Peterson et al., 1999; Wiens & Graham, 2005). The niche similarity tests between YP-VS vs MPS-VS showed little niche overlap suggesting that, although both SDTF patches share more ecological characteristics in common than expected by chance in the environmental space, these are limited by different sets of environmental variables that restrict their geographic distribution (Broennimann et al., 2012). Since MPS-YP VS encompass both SDTF main patches in Mesoamerica, we expected higher niche overlap values with YP-VS and MPS-VS, as a reciprocal trait of niche conservatism (Wiens & Graham, 2005; Wiens, 2011). Yet, our results showed that only YP/MPS-VS and MPS-VS have high degree of niche overlap (> 0.8 in both niche similarity indexes), which suggest that the differences in the environmental niche of both patches may be attributed to differences in geographic extension (Brown & Carnaval, 2019), as the shared areas (both ecological and geographical) between MPS/YP-VS and MPS-VS (i.e., MPS SDTF) are more extensive than those with YP-VS (i.e., YP SDTF). Thus, the distribution of one patch cannot be implied by the distribution of the other: models from MPS species and those with disjunct distribution (YP and MPS) predicted suitable environmental areas in northwest of YP, but models of endemic species to the YP are not reciprocal with the prediction.

Our results for background similarity tests indicate that for most cases (except for *G. velox* and *M. mexicanus*) our studied species occupy different environmental niches than their VS distributional counterpart. This latter suggests that the distribution range of these species may be defined also by other abiotic or biotic features not captured by the assumed reality of VS models. For the endemic species to the YP, environmental niche dissimilarity regarding YP-VS can be attributed to differences in habitat occupation. Both *C. nigrogularis* and *C. yucatanicus*, unlike YP-VS, are not restricted to SDTF, so their niches do not overlap with the VS as they may be found in habitats with different climatic conditions (Barker, 2007; Botts et al., 2012; Slatyer et al., 2013; Williford et al., 2014). The currently widespread distribution of *C. nigrogularis*, which extends from YP southwards to eastern Central America, suggest a broader niche than YP-VS, as predicted by the niche breadth hypothesis (i.e., positive correlation between geographical distribution and niche breadth; Boulangeat et al., 2011; Botts et al., 2012; Slatyer et al., 2013). This is reflected in the wider calibration area of *C. nigrogularis* than YP-VS, which includes fragments of moist evergreen forests in the southern YP. In contrast, the restricted narrow niche width of *C. yucatanicus*, is consistent with a specialist species (Devictor et al., 2008; Serrano-Rodríguez et al., 2018), as reflected on its limited distribution. Our results therefore support the role of climatic niche divergence on shaping the YP biota as further result of historical climatic fluctuations that first isolated populations and promoted genetic divergence afterwards.

For the disjunctly distributed species in MPS and YP SDTF, we find two possible patterns of niche similarity regarding their VS distributional counterpart. On the one hand, the observed environmental niche between *G. velox* and YP/MPS-VS was more similar than expected by chance, suggesting niche conservatism (Broennimann et al., 2012; Brown & Carnaval, 2019). On the other hand, we found niche dissimilarity for *A. rutila* and YP/MPS-VS, suggesting that the VS does not convey the environmental drivers of *A. rutila* range. This may be in line with the proposal of Vázquez-López et al. (2021), in which *A. rutila* should be separated into at least three distinct taxa. Although our ecological niche analysis does not fully support these results, our observed dissimilarity of the environmental niche with YP/MPS-VS support the idea that allopatric populations of *A. rutila* might not retain their ecological niches. This general pattern has also been reported for other birds, such as the *Arremon brunneinucha* complex (Moreno-Contreras et al., 2020).

For species currently endemic to the MPS SDTF with fossil record on YP, the niche dissimilarity of *F. cyanopygius* with MPS-VS is reflected in low number of overlap areas, which suggest that the VS does not fully convey the environmental drivers of the *F. cyanopygius* range. We propose two hypothesis to explain the absence of *F. cyanopygius* in the YP region: 1) the described fossil may represent an extinct and likely closely-related species, and the paleodistribution models were able to predict its potential distribution due to phylogenetic niche conservatism (Peterson et al., 1999; Wiens & Graham, 2005; Pyron et al., 2014); or, 2) its extinction in the YP is explained due to the loss of its environmental niche over time (Peterson et al., 2011), as suggested by the MOP analysis (e.g. lost and niche dissimilarity regarding the VS). The first hypothesis is based on the current absence of other *Forpus* species in most of Mesoamerica and southern Central America. As a widely distributed genus across the Neotropics, *Forpus* is expected to be able to exploit a wide variety of habitats (Smith et al., 2013), it is therefore feasible that a currently extinct species of *Forpus* would have been present in the YP and Central America lowlands in the past. However, our findings support the extinction of the YP taxon due to niche divergence promoted by environmental changes (Hillesheim et al., 2005; Bush et al., 2009; Correa-Metrio et al., 2013; Cruz et al., 2016). Therefore, the YP population of *F. cyanopygius* went extinct because it was unable to adapt to novel conditions (Peterson et al., 2011; Wiens, 2011), nor was able to track its environmental niche through the geographic space (Davis & Shaw, 2001; Martinez-Meyer et al., 2004; Wiens & Graham, 2005; Peterson et al., 2011). On the other hand, the niche similarity between *M. mexicanus* and MPS-VS indicates that both have similar environmental requirements, which explains the high area overlap between both models. These models predict suitable environmental conditions in the northwest YP across all temporal scenarios, suggesting that the YP maintained suitable environmental conditions for *M. mexicanus* at least since the LIG. Therefore, the extinction of *M. mexicanus* from the YP could not be attributed to abiotic factors since the ecological conditions in the region meet the ecological requirements of this species. This suggest that its extinction may be attributed to a lack of response in physiological or behavioral traits (Peterson et al., 2011), to biotic factors, or to both.

In summary, our results show that the currently SDTF fragmented distribution likely involves long evolutionary timescales that have shaped distributional patterns in which the

ecological niche conservatism or divergence may determine species richness and endemism within each SDTF patch. Although high numbers of endemic species found in these areas might be the result of long periods of geographic isolation (that produced strong population genetic signatures) and limited dispersal for taxa, it seems also plausible that it has resulted from ecological niche evolution reflected in recent and rapid evolution/adaptation (allowing persistence of species) to climate changes during glacial periods. The observed patterns identified by our models may be used as hypotheses that can be tested through detailed phylogeographic studies of different taxonomic groups.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available from the first author upon request.

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SUPPORTING INFORMATION

S1. Percentage of contribution importance of climatic variables used for each species.

Underlined values represent the highest contribution percentage for each species.

S2. Mean mobility-oriented parity (MOP) tests for both species and virtual species.

S3. Environmental variables, and mean and standard variation values used to define the climatic niche tolerance of the VS.

BIOSKETCH

Pak Tsun Chan is broadly interested in the structure and evolution of distributional patterns of birds associated with Mesoamerican dry forests. This article constitutes part of the requirements for the M.Sc. degree at Universidad Nacional Autónoma de México (UNAM). He and the other authors collaborate on origin and maintenance of Mesoamerican bird biodiversity based at the UNAM and INAH.

Author contributions: PTC and LAS-G, conceived the ideas; PTC and DAP-T analyzed the data; and PTC and LAS-G lead the writing with assistance from DAP-T and JA-C.

SUPPLEMENTARY INFORMATION 1

Table S1. Percentage of contribution importance of climatic variables used for each species. Underlined values represent the highest contribution percentage for each species.

| Variables | Bird species | | | | | | Virtual species | | |
|--------------------------------------|-----------------------|------------------------|-----------------|------------------|-----------------------|---------------------|-----------------|-------------|-----------|
| | <i>C. yucatanicus</i> | <i>C. nigrogularis</i> | <i>G. velox</i> | <i>A. rutila</i> | <i>F. cyanopygius</i> | <i>M. mexicanus</i> | YP-VS | YP/MPS-VS | MPS-VS |
| Annual mean temperature | | | | | | | | | <u>35</u> |
| Mean Diurnal Range | | | <u>35.7</u> | 18.9 | 5.4 | 3.3 | 5.3 | <u>20.1</u> | 1.4 |
| Isothermality | | 22.6 | 3.5 | <u>25.3</u> | 7.6 | 3.5 | 1.9 | 12.5 | 0.3 |
| Temperature seasonality | 6.7 | | 11.6 | 7.2 | | <u>34.2</u> | | | 21.8 |
| Minimum temperature on coldest month | | 8.3 | | | | | | | |
| Mean temperature of wettest quarter | 4.4 | 2.2 | | | | | 11.4 | 7.7 | |
| Mean temperature of driest quarter | | 3.3 | 17.5 | 8.4 | 20.9 | 21 | 1.2 | 19.6 | |
| Mean temperature of coldest quarter | | 12.2 | | | | | 2.6 | | |
| Annual precipitation | | | | | 9.4 | 2.3 | 9.6 | | |
| Precipitation of wettest month | <u>60.3</u> | <u>41.9</u> | | 3.9 | | | | 2.5 | |
| Precipitation of driest month | 22.5 | | 5.5 | 15 | 1.6 | 6.5 | 17.9 | 9.4 | 18.8 |
| Precipitation seasonality | | 5.5 | 2 | 16.2 | 4.5 | 12.7 | | 7.1 | 3.8 |
| Precipitation of wettest quarter | | | 14.5 | | | | | | 4.6 |
| Precipitation of driest quarter | | | | | 4.8 | | | | |
| Precipitation of warmest quarter | 4.6 | 3.9 | 1.8 | 3.6 | <u>35.1</u> | 2.9 | 2.8 | 10.1 | 7.7 |
| Precipitation of coldest quarter | 1.5 | | 7.9 | 1.6 | 10.6 | 13.6 | <u>47.3</u> | 10.9 | 6.6 |

SUPPLEMENTARY INFORMATION 2

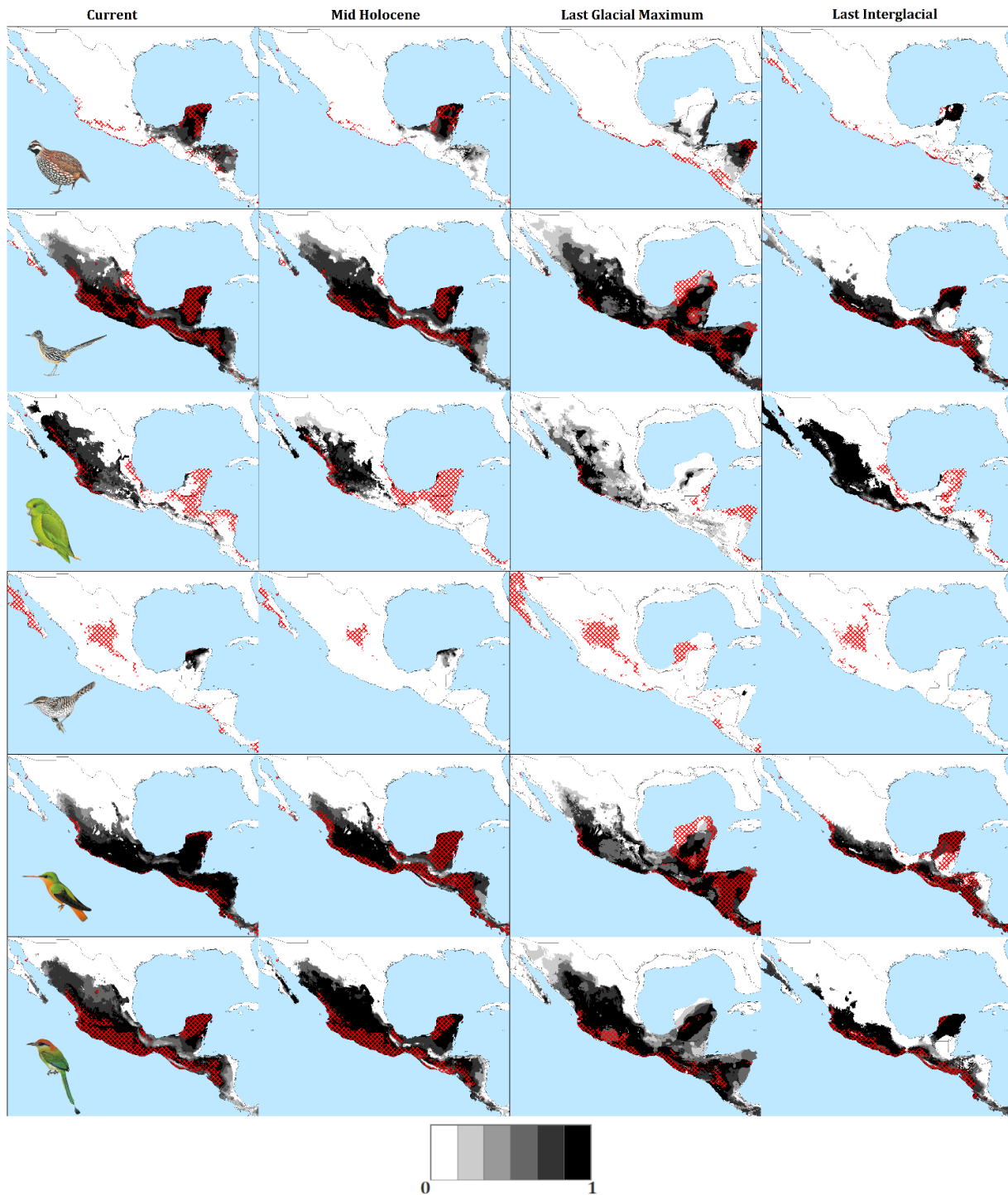


Fig. S1. Mean mobility-oriented parity (MOP) test of *C. nigrogularis*, *G. velox*, *F. cyanopygius*, *C. yucatanicus*, *A. rutila* and *M. mexicanus* to evaluate the existence of areas of strict extrapolation in past scenarios. The analysis was performed considering random sampling of 10% of the M surface. Similarity values to M for MOP calculations for the Mid Holocene and Last Glacial Maximum were obtained considering the average from CCSM4, MIROC-ESM, and MPI-ESM-P global climate circular models. Red polygons correspond to potential distribution areas predicted for each temporal scenario. The grey scale indicates values of strict extrapolation (closer to 0) and similar to present (closer to 1).

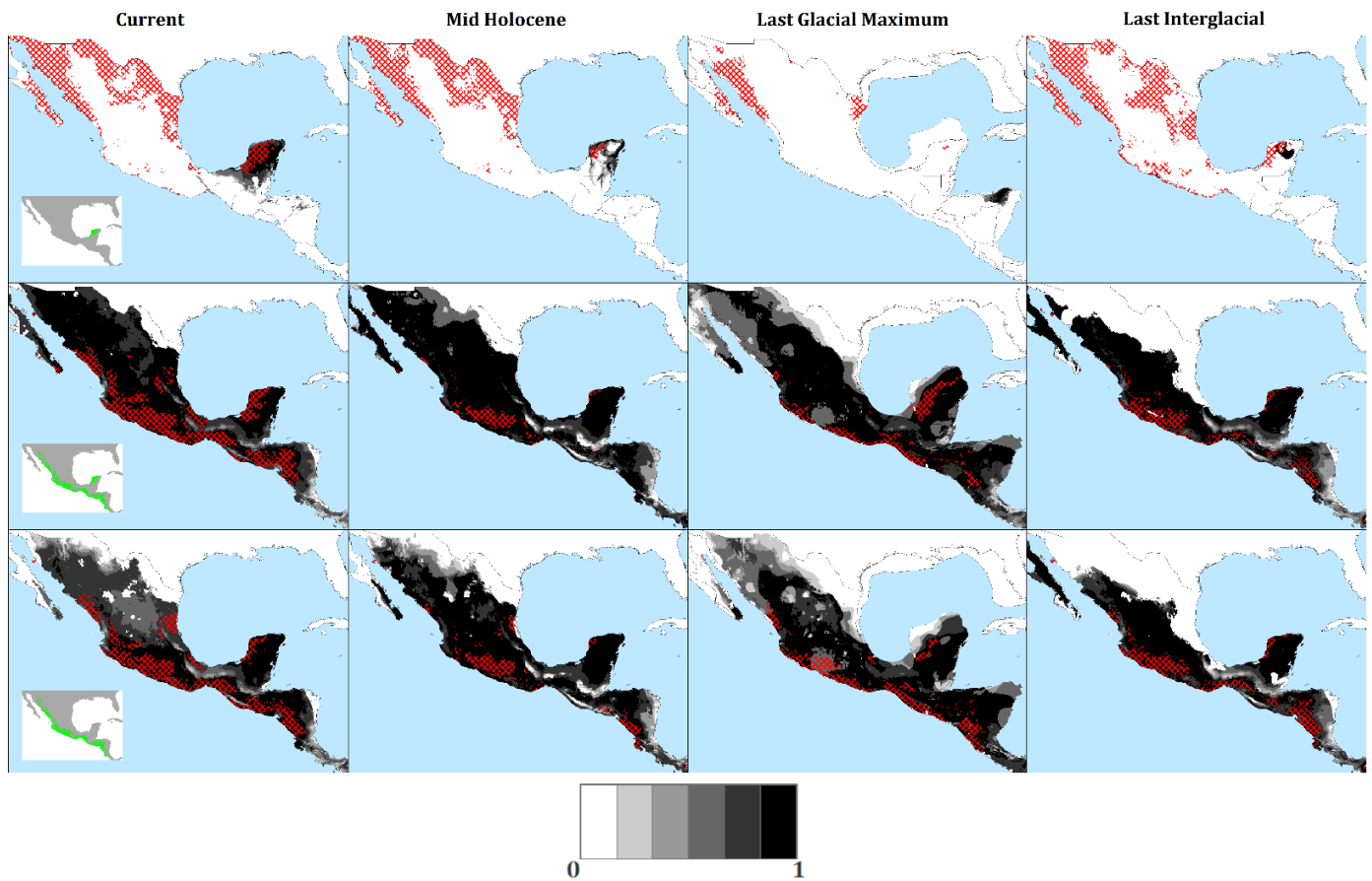


Fig. S2. Mean mobility-oriented parity (MOP) test of the virtual species (from top to bottom: YP-VS, YP/MPS-VS and MPS-VS) to evaluate the existence of areas of strict extrapolation in past scenarios. The analysis was performed considering random sampling of 10% of the M surface. Similarity values to M for MOP calculations for the Mid Holocene and Last Glacial Maximum were obtained considering the average from CCSM4, MIROC-ESM, and MPI-ESM-P global climate circular models. Red polygons correspond to potential distribution areas predicted for each temporal scenario. The grey scale indicates values of strict extrapolation (closer to 0) and similar to present (closer to 1).

SUPPLEMENTARY INFORMATION 3

Table S2. The environmental variables, their mean and standard deviation values used to define the climatic niche tolerance of the VS. These values were based on the sampling of 10000 points around the Mesoamerican SDTF.

| Bioclimatic variable | Mean and standard deviation | Units |
|---|------------------------------------|--------------|
| Mean diurnal range | 13.20 ± 2.43 | Celsius |
| Isothermality | 67 ± 7.07 | Percentage |
| Mean temperature of driest quarter | 23.22 ± 2.90 | Celsius |
| Precipitation of driest month | 9 ± 11.16 | Millimeters |
| Precipitation seasonality | 93.41 ± 19.19 | Percentage |
| Precipitation of warmest quarter | 353 ± 146.54 | Millimeters |

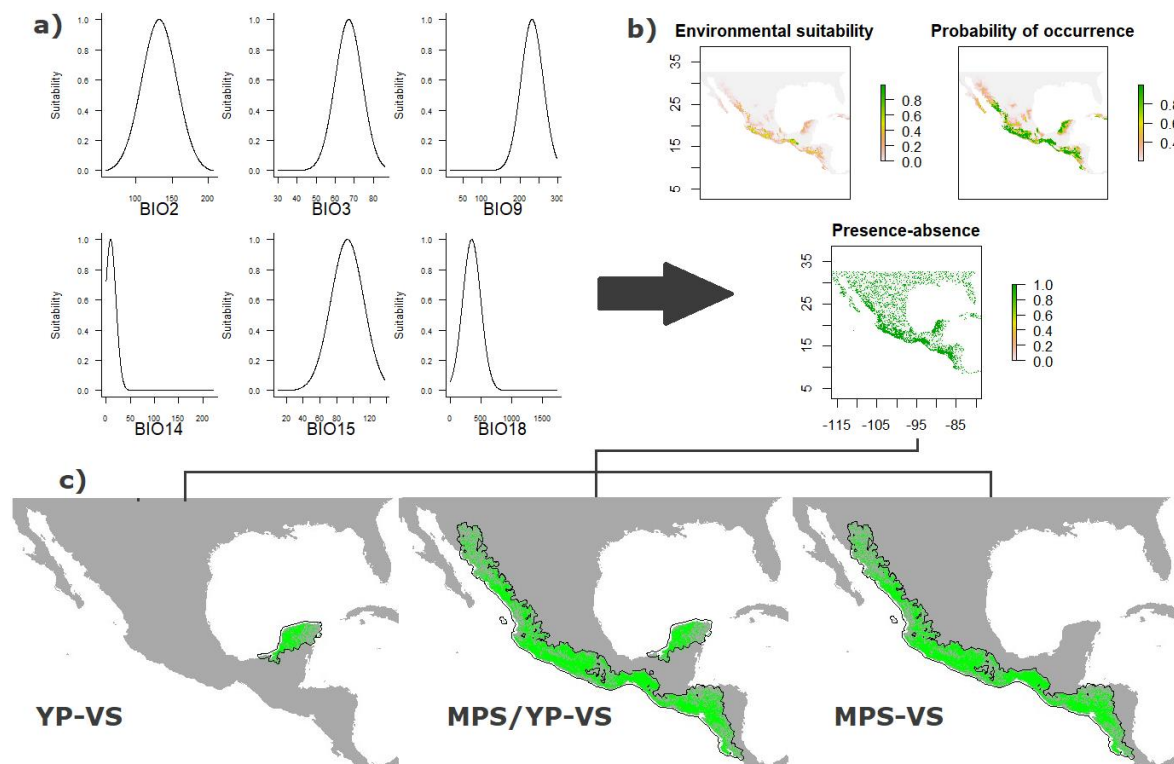


Fig S3. Response curves used to define the responses of the virtual species. A) the responses were defined as normal distribution and were then combined multiplicatively to create a unique environmental suitability-probability of occurrence relation. B) These responses were transformed into a binary presence-absence map by defining a logistic conversion of the environmental suitability. C) This distribution was biased to simulate and match the distribution of the three studied distributional patterns of bird species endemic to Mesoamerican SDTF. The sampling of the virtual species was based on sampling of 1,000 points around a surrounding polygon (delimited in black) for each patch.

DISCUSIÓN GENERAL Y CONCLUSIONES

Diferentes estudios sobre patrones bióticos en el Neotrópico han sugerido que los fragmentos de bosques seco en el continente americano poseen una historia evolutiva propia, lo que ha promovido niveles altos de diversidad y endemismo en diferentes taxones a pesar de la similitud en cuanto a características ambientales (Pennington et al, 2000; Porzecanski & Cracraft, 2005, Ríos -Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres et al., 2018a, 2019b). Sin embargo, algunas especies asociadas a estos bosques están ampliamente distribuidas y se distribuyen en diferentes parches (García-Trejo & Navarro-Sigüenza, 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres et al., 2018a, 2019b), lo que sugiere que la similitud ambiental también permite la persistencia de la especie, debido al conservadurismo de nicho (Peterson et al., 2011), el cual puede ser estable a largo plazo en términos de distribución geográfica (Peterson et al., 2011). Dado que se sugiere que los procesos de adaptación son más lentos que los procesos de extinción (Holt & Gomulkiewicz, 1996), se espera que las especies ampliamente distribuidas muestren un conservadurismo de nicho, lo que implica que la ausencia de conservadurismo puede llevar a las especies a adaptarse a ambientes subóptimos, a desarrollar respuestas ante las nuevas condiciones ambientales, o la extinción local si las especies son incapaces de rastrear o encontrar condiciones apropiadas adecuadas en la geografía (Holt, 1990).

Los modelos de paleodistribución, tanto los modelos de las aves como las especies virtuales mostraron que las áreas potenciales predichas en la PY y VPM se habrían mantenido separados desde al menos el Último Interglacial (120k años), ya que nuestros resultados no apoyan la distribución extendida de bosques secos mesoamericanos en tiempos recientes debido a la no conectividad entre los parches que mostraron nuestros modelos.

El análisis MOP mostró que la mayoría de las áreas geográficas predichas para las especies endémicas de PY (*C. nigrogularis*, *C. yucatanicus* y YP-VS) no son análogas ambientalmente al área de calibración (o “M”), durante el UMG. En cambio, las condiciones ambientales análogas se encontraron altamente restringidas a lo largo de las costas extendidas, pero actualmente sumergidas, del este de América Central (S2); sin embargo, los

altos valores de extrapolación pueden explicarse, en parte, por la presencia de un mosaico de vegetación en el PY durante este tiempo, el cual no es análogo con la vegetación del presente en la península (Cruz et al., 2016) con condiciones relativamente húmedas en el sur (Bush et al., 2009; Correa-Metrio et al., 2012; Hodell et al., 2008; Metcalfe et al., 2000), mayores niveles de precipitación en el centro de la península (Brenner et al., 2002; Cruz et al., 2016; Metcalfe et al., 2000) y patrones de lluvia diferentes comparados con el presente (Hodell et al., 2008). Los cambios en la extensión y distribución geográfica de las áreas idóneas (como en *C. nigrogularis*) sugieren que las especies endémicas pudieron haber “rastreado” condiciones ambientales adecuadas que consecuentemente permitieron su persistencia en la región durante estos períodos.

Para *C. yucatanicus*, las condiciones más áridas y secas en el norte durante el UMG permitieron su expansión hacia el área emergida de la PY, mientras que lo contrario pudo haber ocurrido para *C. nigrogularis*, cuando los bosques húmedos se expandieron en respuesta a los períodos húmedos alrededor del sur y el centro de la península, restringiendo su distribución potencial (Williford et al., 2016). Para ambas especies, las fluctuaciones en los patrones de lluvia pudieron haber influido en sus distribuciones potenciales durante este período, ya que la distribución de estas dos especies es influenciada en gran medida por la cantidad de precipitación (S1). Se predijo una mayor idoneidad ambiental después del Holoceno, luego del establecimiento gradual de condiciones ambientales similares a las actuales en el YP (Brenner et al., 2002; Carrillo-Bastos et al., 2010; Metcalfe et al., 2000). Este resultado coincide con estudios filogeográficos de plantas (Montalvo-Fernández et al., 2018) y mamíferos (León-Tapia, 2020) de la región.

Nuestros modelos para YP-VS respaldan la falta de condiciones adecuadas en escenarios pasados para endémicas de la PY: una especie virtual calibrada con las condiciones ambientales actuales de los bosques secos de la PY no encontró áreas idóneas durante el UMG en la península, porque condiciones ambientales análogas pudieron estar sumamente limitadas o inexistentes. Esto sugiere que el rango de distribución de una especie endémica de los bosques secos de la PY sería muy limitado durante este período, o quizás no podrían existir especies endémicas en estos bosques. Esto último está respaldado por el hecho

de que, a pesar de niveles altos de endemismo en PY (Cortés-Ramírez et al., 2012; Paynter, 1955), la mayoría de las especies endémicas no están restringidas ecológicamente a los bosques secos (Cortés-Ramírez et al., 2012; Paynter, 1955; White & Hood, 2004). Esto puede explicarse por la edad relativamente reciente de los bosques secos de PY (Becerra, 2005; Vázquez-Domínguez & Arita, 2010), que no han estado aislado el tiempo suficiente como para permitir la diferenciación de especies (Cortés-Ramírez et al., 2012). Sin embargo, estudios filogenéticos recientes han reconocido algunas especies conespecíficas de aves que habitan en la PY como especies completas (ej., *Campylorhynchus yucatanicus*: Barker, 2007; *Polioptila albiventris*: Smith et al., 2018). Estos eventos de especiación son consistentes con episodios de aislamiento poblacional y divergencia climática (McCormack et al., 2010) debido a diferencias en condiciones climáticas de la península (Estrada-Loera, 1991), el cual es consistente con nuestras pruebas de equivalencia y similitud de nicho. Estas diferencias climáticas pudieron haber promovido la divergencia genética en algunos taxones (p. ej., la tijereta mexicana *Doricha eliza*: Licona-Vera & Ornelas, 2014; o el tlacuahín *Tlacuatzin canescens*: Arcangeli et al., 2018), así como cambios en el tamaño corporal en algunas especies de aves (Silva-Martínez et al., 2023). Por tanto, las áreas idóneas restringidas predichos en nuestros modelos, junto con condiciones ambientales no análogas en escenarios pasados para YP-VS, son consistentes con estos eventos, subrayando la influencia de procesos ambientales para la determinación de la biota del PY (Duno-de Stefano et al., 2012; Vázquez -Domínguez & Arita, 2009).

Encontramos menos variación en las áreas idóneas predichas para las especies con distribución disyunta y para especies endémicas del VPM. Nuestra proyección hacia el UMG coincide en su mayoría con áreas climáticamente estables y zonas de rupturas filogeográficas reportadas previamente en estudios filogeográficos de aves endémicas (Arbeláez-Cortés et al., 2014; Castillo-Chora et al., 2021a). De igual manera, se encontraron áreas climáticamente estables estimadas entre Nayarit-Jalisco para *G. velox*, *A. rutila*, *F. cyanopygius* y YP/MPS-VS, y es consistente con otras especies de aves (Castillo-Chora et al., 2021a; Vázquez-López et al., 2021), así como otros animales (Demastes et al., 2002; Dewitt et al., 2008). Las áreas climáticamente estables predichas para *M. mexicanus* y su contraparte virtual (MPS-VS) son consistentes con los resultados de Arbeláez-Cortés et al., (2014), quienes propusieron que la

estructura filogeográfica marcada en esta especie es el resultado de rupturas filogeográficas concordantes a lo largo de las tierras bajas del Pacífico, el cual sugiere una diferenciación de haplogrupos más antigua.

Los modelos de YP/MPS-VS y MPS-VS predijeron patrones temporales y espaciales similares. En particular, la contracción de la cuenca del Balsas (Flores-Tolentino et al., 2021) durante el Último Interglacial (UIG) y Holoceno medio (HM), y su posterior expansión durante el UMG y el presente se asemeja a la Hipótesis de Refugio Interglacial, el cual sugiere que la distribución de algunas especies de zonas áridas se contrajeron a refugios cálidos/húmedos durante los periodos interglaciares, mientras que lo contrario ocurrió en el UMG cuando se expandieron en respuesta al clima frío/seco del UMG (Contreras-Negrete et al., 2021; Cornejo-Romero et al., 2017). Por otra parte, encontramos el patrón inverso para *G. velox*, *A. rutila* y *F. cyanopygius*, el cual se asemeja vagamente a la Hipótesis de los Refugio Glaciales, en la que postula que las distribuciones de las especies se contrajeron a diferentes refugios durante los períodos glaciales fríos/secos para posteriormente expandirse durante los períodos interglaciares cálidos/húmedos (Avice & Walker, 1998; Cornejo-Romero et al., 2017; Hewitt, 2000). Ambos patrones describen la dinámica demográfica de las plantas neotropicales de zonas áridas (Contreras-Negrete et al., 2021; Cornejo-Romero et al., 2017; Montalvo-Fernández et al., 2019; Ornelas et al., 2018).

En cuanto a las especies actualmente endémicas de los bosques secos del VPM, las áreas idóneas que indican nuestros modelos coinciden espacialmente con la localidad fósil en el PY (Chan, 2018), para ambas especies, en donde sugieren dos patrones de contracción del rango durante el LGM. Considerando que los fósiles recolectados corresponden al periodo del Pleistoceno-Holoceno, su probable presencia en la península antecede a esta época, como sugieren nuestras proyecciones durante el UIG y UMG. Para *F. cyanopygius*, la contracción del rango en el VPM coincide con las áreas predichas de estabilidad climática de algunas aves endémicas de la región (Arbeláez-Cortés et al., 2014; Arbeláez-Cortés & Navarro-Sigüenza, 2013; Castillo-Chora et al., 2021a), mientras que el desplazamiento hacia el sur de la población de la PY también se ha documentado para otros taxones (Castillo-Chora et al., 2021b; Montalvo-Fernández et al., 2019). Para *M. mexicanus*, encontramos áreas

climáticamente estables a lo largo del VPM (Arbeláez-Cortés et al., 2014), mientras que las condiciones adecuadas para la población de la PY, al igual que MPS-VS, estaban restringidas hacia la parte norte más árida de la península (Paynter, 1955), el cual es un patrón que no ha sido documentado previamente para estudios de paleodistribución o filogeografía de taxones de la península.

Nuestras pruebas de nicho ambiental entre las EV sugieren que, aunque los nichos ambientales no son idénticos o equivalentes, sus nichos observados son más similares de lo esperado por el azar como se, comúnmente observado para especies con poblaciones alopátricas (Figuroa-Corona et al., 2022; Gutiérrez-Zuluaga et al., 2021; Peterson et al., 1999; Wiens & Graham, 2005).

Las pruebas de similitud de nicho entre YP-VS y MPS-VS mostraron poco solapamiento de nicho, lo que sugiere que, aunque ambos bosques secos comparten más características ecológicas en común que lo esperado por el azar en el espacio ambiental, estos están limitados por diferentes conjuntos de variables ambientales los cuales restringen su distribución geográfica (Broennimann et al., 2012). Dado que YP/MPS-VS abarca los parches tanto de la PY como la VPM, se esperaban valores de superposición de nicho más altos con YP-VS y MPS-VS, como un rasgo recíproco del conservadurismo de nicho (Wiens, 2011; Wiens & Graham, 2005). Sin embargo, nuestros resultados mostraron que solo YP/MPS-VS y MPS-VS tienen un alto grado de superposición de nicho (>0.8 en ambos índices de similitud de nicho), lo que sugiere que las diferencias en el nicho ambiental de ambos parches pueden atribuirse a diferencias en la extensión geográfica (Brown & Carnaval, 2019), ya que las áreas compartidas entre YP/MPS-VS y MPS-VS son más extensas que YP/MPS-VS y YP-VS. Estos valores bajos de solapamiento de nicho son consistentes con los MDP de las EV, ya que los modelos de YP/MPS-VS y MPS-VS predijeron áreas idóneas para el noroeste de YP, pero los modelos de YP-VS no predicen áreas idóneas a lo largo del VPM. Por lo tanto, la distribución de un parche no está implícita por la distribución del otro.

Nuestros resultados para la similitud de background entre las especies de aves contra su contraparte distribucional virtual indican que todas las especies de aves, excepto *G. velox*

y *M. mexicanus*, ocupan nichos ambientales diferentes a los de VS, lo que sugiere que la distribución geográfica de estas especies puede estar definido por otras características abióticas o bióticas que no fueron capturadas por la realidad supuesta de los MDP de las EV.

Para las especies endémicas de la PY, la disimilitud del nicho ambiental con respecto a YP-VS puede atribuirse a diferencias en la ocupación del hábitat. Tanto *C. nigrogularis* como *C. yucatanicus*, a diferencia de YP-VS, no están restringidas únicamente a los bosques secos de la península, por lo que sus nichos no se sobrelapan con la EV, ya que estos pueden encontrarse en hábitats con diferentes condiciones climáticas diferentes o más amplias (Barker, 2007; Botts et al., 2012; Slatyer et al., 2013; Williford et al., 2014). La distribución actual de *C. nigrogularis*, el cual se extiende desde PY hacia el este de América Central, sugiere un nicho ecológico de mayor amplitud que YP-VS, como lo esperado en la hipótesis de la amplitud del nicho (correlación positiva entre la distribución geográfica y la amplitud del nicho; Botts et al., 2012; Boulangeat et al., 2011; Slatyer et al., 2013). Esto se refleja en el área de calibración más amplia de *C. nigrogularis* comparado con YP-VS, el cual incluye fragmentos de bosques perennifolios al sur de la PY. En contraste, el nicho ambiental tan restringido o limitado de *C. yucatanicus* es consistente con una especie especialista ecológicamente (Devictor et al., 2008; Serrano-Rodríguez et al., 2018), el cual se refleja en su distribución tan limitada. Por lo tanto, nuestros resultados resaltan la importancia de la divergencia del nicho climático en la configuración de la biota de la PY como resultado de las fluctuaciones climáticas históricas y sistemáticas que primero aislaron las poblaciones de las especies y luego promovieron su divergencia genética.

Para las especies distribuidas de forma disyunta en los bosques secos de la PY y la VPM, encontramos dos patrones de similitud de nicho con respecto a su contraparte distribucional VS. Por un lado, el nicho ambiental observado entre *G. velox* y YP/MPS-VS fue más similar de lo esperado por el azar, lo que sugiere conservadurismo de nicho entre ambas especies (Broennimann et al., 2012; Brown & Carnaval, 2019). Por otro lado, encontramos disimilitud de nicho para *A. rutila* y YP/MPS-VS, lo que sugiere que la EV no refleja los limitantes ambientales que delimitan la distribución geográfica de *A. rutila*. Esto apoya la propuesta de Vázquez-López et al. (2021), en donde consideran los autores que esta

especie debería separarse en al menos tres taxones distintos. Aunque nuestro análisis de nicho ecológico no respalda completamente estos resultados, la disimilitud observada del nicho ambiental con YP/MPS-VS respalda la idea de que las poblaciones alopátricas de *A. rutila* en la PY y VPM podrían no conservar sus nichos ecológicos.

Para las especies actualmente endémicas de la VPM con registro fósil en la PY, la disimilitud de nicho de *F. cyanopygius* con MPS-VS se refleja con un bajo número de áreas idóneas sobrelapadas, lo que sugiere que la EV no refleja los limitantes ambientales de la distribución geográfica de *F. cyanopygius*. Proponemos dos hipótesis para explicar la ausencia o extinción de *F. cyanopygius* en el PY: 1) los materiales fósiles descritos pueden representar una especie hermana extinta, y los modelos de paleodistribución pudieron predecir su distribución potencial como producto de conservadurismo del nicho filogenético (Peterson et al., 1999; Pyron et al., 2014; Wiens & Graham, 2005); o, 2) su extinción en la PY se explica por la pérdida de su nicho ambiental a lo largo del tiempo (Peterson et al., 2011), como se sugiere el análisis del MOP (e.g. pérdida y disimilitud de nicho con respecto a la EV). La primera hipótesis se basa en la ausencia actual de otras especies de *Forpus* en la mayor parte de Mesoamérica y el sur de Centroamérica. Como un género ampliamente distribuido en el Neotrópico, se espera que *Forpus* pueda explotar una amplia variedad de hábitats (Smith et al., 2013), por lo tanto, es factible que una especie actualmente extinta de *Forpus* pudo persistir en la PY y las tierras bajas de América Central en el pasado. Sin embargo, nuestros hallazgos respaldan la extinción local de la PY debido a la divergencia de nicho promovida por cambios ambientales (Bush et al., 2009; Correa-Metrio et al., 2013; Cruz et al., 2016; Hillesheim et al., 2005). Por lo tanto, la población de la PY de *F. cyanopygius* se extinguió porque no pudo adaptarse a nuevas condiciones (Peterson et al., 2011; Wiens, 2011), y tampoco pudo rastrear o perseguir su nicho ambiental idóneo a través del espacio geográfico (Davis & Shaw, 2001; Martinez-Meyer et al., 2004; Wiens & Graham, 2005; Peterson et al., 2011). Por otro lado, la similitud de nicho entre *M. mexicanus* y MPS-VS indica que ambos tienen requisitos ambientales similares, lo que explica el alto sobrelape de áreas idóneas entre ambos modelos. Los modelos de ambas especies predicen condiciones ambientales adecuadas en el noroeste de la PY durante todos los escenarios temporales, lo que sugiere que la PY mantuvo condiciones ambientales adecuadas para *M. mexicanus* al

menos desde el UIG. Por lo tanto, la extinción de *M. mexicanus* del PY no podría atribuirse a factores abióticos, ya que esta región tiene condiciones ecológicas que cumplen con los requerimientos ecológicos de esta especie. Esto sugiere que su extinción puede atribuirse a una falta de respuestas fisiológicas o de comportamiento (Peterson et al., 2011), u otros factores bióticos no considerados en los modelos.

En resumen, nuestros resultados muestran que la distribución fragmentada actual de los bosques secos mesoamericanos es el resultado de escalas evolutivas de tiempo, en donde cada núcleo de parche pudo formar riqueza de especies y endemismo dentro de cada parche de bosque. Aunque el alto número de especies endémicas que se encuentran en estas áreas podría ser el resultado de largos períodos de aislamiento geográfico (lo que produjo fuertes firmas genéticas de la población), la edad del ecosistema y la dispersión limitada de los taxones de estudio, parece plausible que también sea el resultado de una evolución y adaptación reciente y rápida (el cual permitió la persistencia de las especies) a los cambios climáticos durante los períodos glaciales. Nuestros resultados proporcionan información relevante sobre el papel de los factores geográficos y ecológicos en la evolución, diversificación y distribución de la avifauna de bosques secos mesoamericanos. Sin embargo, los patrones observados identificados por nuestros modelos pueden usarse como hipótesis que pueden probarse a través de estudios filogeográficos detallados de diferentes grupos taxonómicos.

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