UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
BIOLOGÍA EVOLUTIVA

PATRONES Y PROCESOS DE DIVERSIFICACIÓN EN AVES ENDÉMICAS DEL OESTE DE MÉXICO

T E S I S

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

P R E S E N T A

ENRIQUE ARBELÁEZ CORTÉS

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México D.F, Noviembre de 2013.

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ASUNTO: Oficio de Jurado

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **2 de septiembre de 2013**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **ARBELÁEZ CORTÉS ENRIQUE** con número de cuenta **508451236** con la tesis titulada: **"Patrones y procesos de diversificación en aves endémicas del Oeste de México"**, realizada bajo la dirección del (la) **DR. ADOLFO GERARDO NAVARRO SIGÜENZA:**

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

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Dra. María del Coro Arizmendi Arriaga
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FACULTAD DE CIENCIAS
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Resumen

El estudio de la variación geográfica de diferentes caracteres permite visualizar la historia reciente de las especies. En particular, identificar los patrones y procesos involucrados en la diversificación intraespecífica de secuencias de ADN es el objetivo de un campo conocido como filogeografía. La comparación de patrones filogeográficos entre especies co-distribuidas permite examinar los procesos comunes que han promovido la divergencia de linajes en una región particular. Sin embargo, identificar tales procesos no es sencillo, y es necesario inferir las condiciones ambientales del pasado y contrastar con eventos geológicos para explicar los patrones observados actualmente. En esta tesis utilicé datos moleculares de varios loci para obtener información sobre la evolución reciente de siete especies de aves (*Phaethornis longirostris / mexicanus*, *Momotus mexicanus*, *Melanerpes chrysogenys*, *Pheugopedius felix*, *Thryophilus sinaloa*, *Vireo hypochryseus* y *Passerina leclancherii*) que pertenecen a cuatro órdenes diferentes y son endémicas del norte del bosque seco neotropical en el oeste de México. Obtuve secuencias del ADN mitocondrial (ND2 y COI o cyt b) y del ADN nuclear (20454, GAPDH, MUSK y TGFB) para al menos un locus de 327 individuos de todas las especies. También realicé modelos del nicho ambiental de algunas especies (ENMs) e incluí medidas morfométricas de otras con el fin de complementar la información molecular.

En general, las siete especies presentaron una estructura filogeográfica significativa. A pesar de que hubo diferencias en el número de haplogrupos definidos para cada especie las zonas de diferenciación filogeográfica estuvieron más o menos en las mismas áreas. Estas coinciden con zonas en las cuales ya existía evidencia de algún tipo de diferenciación biogeográfica para otros taxa. La diferenciación intraespecífica en estas aves del oeste de México probablemente se originó en los últimos 500.000 años. Los patrones filogeográficos encontrados resultan interesantes ya que se mantienen en un área relativamente pequeña y en especies de aves que tienen distribuciones geográficas prácticamente continuas, ya que para otras especies con una distribucion similar usulamente no se encuentra estructura genética. En particular, 1) encontré diferencias del 4.2 % en el ADNmt así como diferentes alelos para un locus del ADNn entre las poblaciones, de *P. longirostris*, del este y del oeste de México, lo cual sumado a la evidencia morfológica soporta la separación de las poblaciones del oeste como la especie *Phaethornis mexicanus*. Sin embargo sólo encontré una estructura filogeográfica incipiente entre las poblaciones de *P. mexicanus*, y los alelos de los loci nucleares fueron compartidos por todos sus individuos. 2) La estructura filogeográfica del ADNmt de *M. mexicanus* presentó tres haplogrupos que mostrarón entre 1.5 y 3.9 % de diferenciación. En contraste, todas las secuencias del locus GAPDH del ADNn fueron las mismas aunque hubo cierta variación en otro loci del ADNn (locus 20454). Las áreas climáticamente estables para esta especie fueron amplias pero interrumpidas en la frontera entre Oaxaca y Guerrero, ajustándose con la división filogeográfica más clara de esta especie. 3) Para *M. chrysogenys* encontré tres haplogrupos en el ADNmt separados por entre 0.6 y 0.8 % de diferencias, y los loci nucleares también presentaron ciertas diferencias geográficas en la frecuencia de sus alelos. Esta especie presentó varias áreas climáticamente estables; algunas de ellas bordeando la región en donde se encontró la mayor divergencia genética (*e.g*., Michoacán). 4)

Vireo hypochryseus presentó dos clados en su ADNmt que tuvieron estructura geográfica, pero los ENMs de esta especie no sugirieron un escenario de fragmentación geográfica en el pasado. Un modelo de aislamiento por resistencia basado en la configuración actual de las condiciones climáticas explicó mejor las distancias en el ADNmt, y las diferencias en tamaño, que un modelo de aislamiento por distancia. 5) *T. sinaloa* y *P. felix* también mostraron una estructura filogeográfica marcada. 6) Para *P. leclancherii* encontré dos haplogrupos en el ADNmt diferenciados por 0.36 % de su secuencia. Aunque la estructura filogeográfica de los loci del ADNn no fué tan clara como en el ADNmt, se pudo observar cierto grado de congruencia entre los dos tipos de marcadores. Adicionalmente, de acuerdo con los ENMs se encontraron dos áreas climáticamente estables, que parcialmente coincidieron con la distribución de los dos haplogrupos.

En conjunto, mis resultados sugieren que ciertas zonas del oeste mexicano han sido climáticamente estables. Lo cual puede puede tener relación con la diversificación intraespecífica de la avifauna de la región al haber permitido la existencia de poblaciones aisladas. Además, mis resultados representan un nuevo patrón, para aves neotropicales, que consiste en estructura filogeográfica en un área relativamente pequeña sin una evidencia clara de barreras que eviten el flujo génico. Estos resultados ponen de manifiesto un caso diferente cuando se comparan con los patrones de disrupciones filogeográficas compartidas entre especies de aves neotropicales con distribuciones amplias, pero divididas por barreras geográficas conspicuas, y también cuando se comparan con los patrones de poca divergencia genética en especies con distribuciones continuas. Debido a que el marco temporal para la diversificación intraespecífica en estas especies es reciente, la actividad geológica en la región, que ocurrió hace más de 3 millones de años, puede ser descartada como el factor que promovió la diversificación. Sin embargo, encontré cierta concordancia entre las disrupciones filogeográficas de algunas especies y la cercanía de elevaciones de más de 1900 m próximas a la costa (<26 km), lo cual sugiere que esas montañas pudieron haber promovido cierto tipo de inestabilidad climática en las tierras bajas. Por lo tanto, propongo un escenario en el cual las fluctuaciones climáticas del Pleistoceno generaron cambios en la distribución de las especies, promoviendo la evolución de diferentes linajes a partir de poblaciones aisladas. Esto es parcialmente soportado por evidencia paleoecológica que indica la ocurrencia de fragmentación del bosque seco neotropical. Sin embargo es pobable que dicha diferenciación haya sido asincrónica entre especies. Mi trabajo contribuye a un cuerpo de evidencia que ha indicado una diversificación activa de linajes endémicos en la parte norte del bosque seco neotropical, y refuerza la idea de que el oeste de México es una región con un alto numéro de endemismos, alberga numerosos taxa con diversas historias, y es así un área importante en la cual estudiar la diversificación reciente de las biotas neotropicales. Mi trabajo también plantea la pregunta sobre qué tipo de cambio ecológico ocurrió en la región que llevó a divergencia poblacional en especies que presentan una gran tolerancia a cambios antropogénicos del hábitat y que exhiben una gran capacidad de dispersión.

Abstract

The study of geographic variation in intraspecific traits provides a window onto the recent history of species. Identifying the patterns and processes involved in the differentiation of DNA sequences is the aim of a field known as phylogeography. The comparisons of phylogeographic patterns among co-distributed species provide insights into the common processes driving lineage divergence in a particular region. However, identifying such processes is not always straight forward, and inferring past environmental conditions and contrasting them with documented geological events is sometimes necessary to explain current patterns. Here I used a multilocus dataset to gain insight into the recent evolution of seven bird species (*Phaethornis longirostris / mexicanus*, *Momotus mexicanus*, *Melanerpes chrysogenys*, *Vireo hypochryseus, Pheugopedius felix*, *Thryophilus sinaloa*, and *Passerina leclancherii*) from four different orders that are all endemic species to the northernmost range of the Neotropical dry forest in western Mexico. I obtained mitochondrial DNA (ND2 and COI or cyt b) and nuclear DNA (20454, GAPDH, MUSK, and TGFB) sequences for at least one locus of 327 individuals across all species. I also determined environmental niche models (ENMs) and included morphometric measurements for some species to complement the molecular information.

In general, all seven species showed a significant phylogeographic structure. Despite differences in the number of haplogroups of each species the obtained phylogeographic breaks occurred roughly in the same areas, which represent zones where biogeographic breaks have been previously found for other taxa. Such an intraspecific differentiation probably originated during the last 500,000 years. The phylogeographic patterns are particularly noteworthy because they occur in a relatively small area and for bird species distributed in almost continuous ranges, while usually bird species with this kind of distribution did not exhibit genetic structure. Particularly, 1) I found differences of 4.2 % in mtDNA as well as different alleles for one nDNA locus between western and eastern populations of *P. longirostirs*. This information added to morphological evidence supported the separation of western Mexican populations as a different species: *Phaethornis mexicanus*. However, I found only a shallow mtDNA phylogeographic structure between populations of *P. mexicanus*, with nuclear alleles shared by all individuals. 2) The mtDNA phylogeographic structure of *M*. *mexicanus* showed three haplogroups which diverged between 1.5 and 3.9 % in their DNA sequence. In contrast, all the sequences obtained for the nDNA marker GAPDH were identical, altough there was some variation in another nDNA locus (locus 20454). The climatic stable areas of this species were broad and disrupted at the Guerrero-Oaxaca border, matching their major phylogeographic break. 3) For *M. chrysogenys* I found three haplogroups with differences in their DNA sequences ranging between 0.6 and 0.8 %; the nuclear loci also showed some geographical differences in their alleles frequencies. This species presented several climatically stable areas, some of them bordering the region where their major genetic divergence was located. 4) *Vireo hypochryseus* showed two mtDNA clades that exhibited a significant geographic structure, but their ENMs did not support a scenario of geographic fragmentation in the past. A model of isolation by resistance based in the actual configuration of climatic conditions explained better the mtDNA distances, and the size differences, than a model of isolation by distance. 5) *T. sinaloa* and *P. felix* also showed a marked phylogeographic structure. 6) For *P. leclancherii*, I found two mtDNA

haplogroups separated by 0.36 % in their sequences. Although the phylogeographic structure of nDNA loci was not as clear as that for mtDNA, some congruence was observed between markers. Besides, according to the ENMs, two climatic stable areas were found, which were partially concordant with the range of the two haplogroups.

Altogether, my results suggest that certain regions of western Mexico have been climatically stable allowing the existence of isolated populations and promoting intraspecifc differentiation. Besides, my results present a new pattern, for Neotropical birds of a significant phylogeographic structure within a relatively small area without any clear evidence of current barriers to gene flow. They highlight a different case when compared to other shared phylogeographic breaks among widespread Neotropical birds with ranges divided by conspicuous geographic barriers combined with a pattern of low genetic divergence in species with continuous distributions. Because the intraspecific differentiation is recent, the geological activity in the region, which dates back to more than 3 million years ago, could be excluded as a factor driver of diversification. However, I found some concordance between the phylogeographic breaks of some species and the proximity of mountains above 1900 m near the coast (<26 km), which suggest that these mountains could be causing some kind of climatic instability in the lowlands. Therefore, I propose a scenario in which Pleistocene climatic fluctuations generated changes in the species ranges, promoting the evolution of different lineages from isolated populations. This scenario is partially supported by paleoecological evidence suggesting fragmentation of the Neotropical dry forests. However, the intraspecific differentiation was likely asyncronous among species. My work contributes to a growing body of evidence indicating an active diversification of endemic lineages in the northern Neotropical dry forest, and reinforces the idea that western Mexico is a hotspot of endemism, home to numerous taxa with diverse histories, and it is thus an important area for the study of recent lineage diversification of Neotropical biotas. My work also raises a question regarding the kind of ecological changes that occurred in the region, which drove population divergence in species with high tolerance to anthropogenic disturbances and high dispersal capacities.

INTRODUCCIÓN

Entender los procesos evolutivos involucrados en el origen de la biodiversidad es uno de los principales objetivos de la biología. Dado que estos procesos dejan 'sus marcas' a diferentes niveles taxonómicos, y en distintas escalas geográficas, son estudiados por diferentes disciplinas. El uso de información molecular de los individuos de una especie permite describir patrones de la variación genética en la geografía, detectar procesos filogenéticos y demográficos y asignar un marco temporal a tales procesos, siendo en conjunto estos análisis los que conforman la filogeografía [1, 2]. El objetivo de la filogeografía es poner a prueba la congruencia entre las historias evolutivas, demográficas y de distribución geográfica de los haplotipos/alelos/linajes contra las características geológicas y ecológicas de una región y determinar la cronología de la diversificación [3]. Para especies que comparten su distribución geográfica, el paradigma es aceptar una historia biogeográfica compartida como la explicación más parsimoniosa y se esperaría encontrar congruencia entre sus patrones filogeográficos (*i.e*., filogeografía comparada) que permitan plantear una narrativa de la historia reciente de una región [4-7]. En este punto es necesario hacer una salvedad ya que patrones filogeográficos similares pueden resultar de diferentes eventos (*i.e*., pseudocongruencia filogeográfica), lo cual es comentado más adelante [4].

Los análisis filogenéticos y filogeográficos basados en información molecular han incrementado el nivel de detalle sobre las historias de especies neotropicales y han permitido establecer un marco temporal alrededor de 4 millones de años (m.a.) para los procesos de especiación y de diferenciación intraespecífica en vertebrados [8-10]. En particular para las aves neotropicales, los estudios filogeográficos se han centrado en zonas de montaña o en las selvas húmedas de las tierras bajas ([4, 11-13] y referencias citadas). Otras regiones biogeográficas con menor riqueza pero con alto endemismo, como los bosques secos del oeste mexicano, están menos representadas.

En México existen alrededor de 100 aves endémicas que corresponden al 10 % de la riqueza de este grupo en el país [14]. A pesar de que existen por lo menos tres estudios filogeográficos incluyendo aves que se distribuyen en el oeste de México [15-17], éstas son especies que no se consideran endémicas de la región. Tambien,

existe información biogeográfica indicando que en el oeste mexicano ha evolucionado, *in situ*, una biota singular. Por ejemplo, hay gran endemimo para aves (45 especies [14]), mamíferos [20-23] y plantas [18] (particularmente para el género *Bursera* con 80 especies [19]). Además, el oeste mexicano se considera un centro de endemismo basal de algunos grupos [24].

El hecho de que en el oeste méxicano una proporción alta de especies de aves sean endémicas lo convierte en un sitio de interés para realizar un estudio comparativo de patrones filogeográficos. Por esta razón seleccioné siete especies de aves, que representaran differentes órdenes taxonómicos y diferentes historias naturales considetando, además, que estuvieran bien representadas en muestras de tejidos o que fueran lo suficientemente comunes para asegurar su muestreo. Las especies que incluyo en mi trabajo son: *Momotus mexicanus* [25], *Phaethornis mexicanus* [26], *Melanerpes chrysogenys* [25], *Vireo hypochryseus* [27], *Passerina leclancherii* [25], *Thryophilus sinaloa* y *Pheugopedius felix*; que pertenecen a seis familias y a cuatro órdenes y tienen entre 2 y 6 subespecies reconocidas [28, 29]. Sus distribuciones geográficas están circunscritas, principalmente, al oeste mexicano y se solapan total o parcialmente. A pesar de representar linajes diferentes de aves estas especies son relativamente parecidas a nivel ecológico ya que se encuentran en elevaciones menores a 2000 m, están mas o menos asociadas al bosque seco caducifolio en donde la mayoría son especies comunes y habitan tanto zonas intervenidas (*e.g*., cultivos) como bosques maduros. No obstante, algunos aspectos de su historia natural son diferentes ([28, 30-34], Arbeláez-Cortés pers. obs). Por ejemplo, unas especies parecen estar restringidas al bosque seco (*M. mexicanus* y *P. leclancherii*) y otras son generalistas en cuanto a su hábitat (*P. mexicanus*, *M. chrysogenys*). Unas tienen hábitos arbóreos (*M. mexicanus* y *M. chrysogenys)*, otras se asocian a vegetación baja o están comúnmente sobre el suelo (*P. leclancherii, V. hypochryseus, T. sinaloa y P. felix*); una es un colibrí no territorial que forrajea activamente en diferentes lugares del bosque (*P. mexicanus*), otra puede considerarse sedentaria (*M. mexicanus*) y otras presentan variaciones estacionales en abundancia (*M. chrysogenys, T. sinaloa y P. leclancherii*).

Patrones filogeográficos en el oeste mexicano

Para el oeste mexicano existen al menos 13 trabajos filogeográficos con diferentes organismos, y a pesar de las diferencias en distribución geográfica y en el esquema de muestreo usados ciertos patrones filogeográficos parecen emerger (Tabla 1). Por ejemplo, la estructura filogeográfica es marcada en peces, anfibios, insectos y reptiles [35-40], pero ausente o incipiente en aves y murciélagos [15-17, 21, 41]. Ciertas zonas como la parte norte del oeste de México (Sonora-Nayarit) parecen tener linajes diferenciados del resto; mientras que en la región entre Jalisco y Chiapas se han encontrado varias disrupciones filogeográficas, principalmente entre Oaxaca y Guerrero (Tabla 1). Los eventos históricos considerados para explicar estos patrones filogeográficos son la vicarianza asociada a la formación del Eje Neovolcánico hace unos 14 a 2,5 m.a., o la diferenciación debida a vicarianza por cambios climáticos entre hace 3 m.a. y 50.000 años (ver Tabla 1 y referencias citadas).

Procesos históricos y patrones biogeográficos en el oeste mexicano

Geológicamente, el oeste de México es heterogéneo [62-64]. Sin embargo, los eventos de mayor interés para entender la biota actual ocurrieron después de que las provincias biogeografías mayores empezaran a formarse en esta zona entre el Oligoceno y mediados del Mioceno durante un periodo de aridez producida por cambios climáticos asociados con intenso tectonismo y vulcanismo mientras se formaban la Sierra Madre Occidental y la Sierra Madre del Sur [37]. Históricamente, los bosques secos estuvieron ampliamente distribuidos, pero se restringieron a las tierras bajas a lo largo de las costas de México luego de la la formación de la Sierra Madre Occidental (hace 46 m.a.) [37], hasta su último levantamiento hace 34 a 15 m.a. [19, 65]. Luego, a mediados del Mioceno (hace 20 a 14 m.a.), se empezó a formar el Eje Neovolcánico, continuando entre hace 5 y 2 m.a.[19, 36, 37]. Esos sistemas montañosos, al bloquear los frentes fríos del norte, permiten que existan las condiciones climáticas que mantienen el bosque seco neotropical. La orogénesis del Eje Neovolcánico parece asociarse con un incremento en la diversificación de *Bursera* un género de plantas característico del bosque seco que presenta máximos de diversificación filogenética entre hace 20 y 10 m.a. [19]. Además, el Eje Neovolcánico, parece haber influido en el patrón filogeográfico de algunas especies

de tierras bajas. Por ejemplo, linajes hermanos de serpientes encontrados a ambos lados del Eje Neovolcánico datan de hace 14 a 7 m.a. [37] y la división de especies de peces, por vulcanismo en las fosas tectónicas (*graben*) de Tepic y de Colima, datan de hace 7 a 3 m.a. [36, 58] (Tabla 1). La formación del Eje Neovolcánico y la presencia de la Sierra Madre del Sur en el Cenozoico [37] cerraron la depresión del Rio Balsas que luego fue dividida por la Sierra de Taxco [35]. Sedimentos lacustres en la región sugieren que depresiones como esta estuvieron periódicamente inundadas y probablemente fueron una barrera a la dispersión de los organismos [37], lo cual pudo generar linajes endémicos en este cañón.

Tabla 1. Estructura filogeográfica y procesos históricos para especies del oeste de México

Taxón	Estructura filogeográfica	Eventos históricos y dataciones	Procesos demográficos	Referencia
Spondias purpurea	((Jalisco, Nayarit, Michoacan) Oaxaca-Chiapas)	N.A	N.A	42
Azteca pittieri	((Jalisco, Guerrero) Oaxaca)	1-2 m.a	Posible vicarianza por contracción del bosque seco	40
Poecilia butleri	(Sinaloa-Nayarit)(Jalisco-Colima)	Vulcanismo en Colima *graben* (5-2.5 m.a.)	N.A.	36
Rana forrieri	((Sonora-Nayarit)(Jalico-Guerrero)(Balsas))(Oaxaca)	Cambios climáticos y geológicos (Sierra de Taxco). Mioceno-Plioceno	N.A.	35
Trimorphodon biscutatus	((Sinaloa)(Jalisco))(Jalisco((Michoacan-Balsas)((Guerrero)(Oaxaca))))	Vicarianza por el Eje Neovolcánico (14-7 m.a)	N.A.	37
Leptodeira maculata-annulata	(Jalisco-Michoacán)(Guerrero-Oaxaca)	Formación de cuencas de ríos y cambios climáticos del Mioceno	N.A.	39
Hypsiglena torquata	(Sinaloa)(Jalisco)	Expansión reciente a través del Eje Neovolcánico	N.A.	43
Ctenosaura pectinata	(Sinaloa)(Jalisco))(Colima)(Balsas)(Guerrero) (Oaxaca)	Clados originados hace 3.1-0.1 m.a	Expansión poblacional	38
Campylorhynchus rufinucha	(Michoacán-Centro Oaxaca)(Este Oaxaca)(Chiapas)	N.A.	Expansión poblacional. Contacto secundario	17
Icterus pustulatus	No muy clara. (Sinaloa-Michoacán)(Michoacán-Guerrero)(Guerrero-Chiapas)	N.A.	Expansión poblacional reciente	16
Cardinalis cardinalis	((Sinaloa-Sonora)(Islas Maria) Otras zonas de México y E.U)(Michoacán-Guerrero-Oaxaca)	N.A	Expansión poblacional al norte, y estabilidad en el resto del área	15
Pteronotus davyi	No	Refugios cerca del Istmo de Tehuantepec, hace 50.000 años	Expansión poblacional reciente	41
Musonycteris harrisoni	No es clara	N.A.	Aislamiento por distancia, Migración	21

Además de los eventos geológicos, los cambios climáticos durante el Pleistoceno en México [66] pudieron también haber afectado los ecosistemas de tierras bajas en el oeste, produciendo la fragmentación del bosque seco dominado por *Bursera*, un grupo de plantas que no toleran temperaturas mínimas absolutas de 0 °C [19]. Existe evidencia de disminuciones en temperatura de hasta 8 °C hace 25.000 años para el Eje Neovolcánico [67]. Adicionalmente, los mapas de vegetación potencial para el Pleistoceno en México, indican que el bosque seco del oeste mexicano estuvo interrumpido por bosque húmedo y bosque de coníferas [68, 69] a la altura del Eje Neovolcánico y en algunos puntos de Guerrero, Michoacán y Oaxaca que podrían relacionarse con las divisiones filogeográficas encontradas en varios taxa (Tabla 1). Hace 13.000 años los cinturones altitudinales de vegetación cambiaron en la Sierra Madre Occidental según evidencias de presencia de bosques de pinos hasta a 1500 m de elevación [70, 71]. También existe evidencia de la ocurrencia de bosques de pinos (7000 a 5000 años atrás) e incursiones marinas (hace 5500 años) en Sinaloa [72], así como de *tsunamis* (hace 3500 años) en la costa de Guerrero [73]. Para la cuenca del río Balsas existen datos de sedimentos que indican que durante los últimos 2700 años se han sucedido periodos de 1000 años en los que el bosque seco ha sido reemplazado por vegetación de bosque mesófilo, que luego ha vuelto a ser reemplazado por bosque seco [74].

Biogeográficamente, el oeste de México ha sido dividido usando información sobre la distribución de algunas aves [75, 76] y del género *Bursera* [77]. En general, para aves, hay una región al norte (Sonora-Sinaloa) y otra zona intermedia desde Jalisco-Colima hasta el centro de Oaxaca que se mezcla con una zona al Sur (Centro de Guerrero - Costa de Chiapas). Para *Bursera* las regiones son más discretas, pero parecen coincidir con el patrón general de las aves, llamando la atención la división de dos áreas por el Eje Neovolcánico. Para *Bursera* la depresión del Balsas es un área de endemismo que no se observa en las aves. Otro estudio usando plantas ha hecho un comentario sobre una división de la región en dos áreas principales que corresponden aproximadamente con las tierras bajas al norte y al sur del eje Neovolcánico [78]. Los patrones filogeográficos de algunas especies estudiadas (Tabla 1) y otras que incluyo en mi investigación parecen coincidir en ciertos puntos con estos patrones biogeográficos.

Planteando preguntas sobre la historia reciente del oeste de México

Si el aislamiento del resto del continente ha sido responsable de la ocurrencia de las aves endémicas, entonces las dataciones moleculares usando filogenias que incluyan especies de la zona deberían indicar un origen posterior a la formación de la Sierra Madre Occidental y de la Sierra Madre del Sur. Además, si solo la vicarianza ha sido responsable de dicha diferenciación un análisis comparando el nicho de estas especies con el de sus especies hermanas debería indicar conservadurismo [79]. Estas hipótesis las pongo a prueba en el primer capítulo usando el complejo de especies *P. longirostris - mexicanus* que presenta poblaciones tanto en las selvas húmedas del este de México como en los bosques secos del oeste [26].

A pesar de la compleja historia del oeste de México y de la evidencia de subdivisiones en su biota, muchas de sus aves endémicas tienen una distribución geográfica continua [28], contrario a lo encontrado en zonas montanas neotropicales, donde las aves tienen poblaciones alopátricas que han sido identificadas como linajes filogeográficos diferentes [4]. Esto permite plantear la hipótesis de que la estructura filogeográfica de las aves del oeste mexicano no es marcada y que de existir debería explicarse principalmente por aislamiento por distancia o aislamiento por resistencia (*i.e.,* distancia que considera la heterogeneidad ambiental del espacio geográfico) [80]. Esta posibilidad la examino para las cuatro especies analizadas en los capítulos dos y tres [25, 27].

Las especies que incluyo en este trabajo muestran estructura filogeográfica que no se explica unícamente por la distancia geográfica-ambiental. En ausencia de una barrera fisiográfica contemporánea que explique esa estructura se puede considerar que es derivada de un evento de vicarianza histórica. La datación de los eventos de diversificación filogeográfica, usando tasas de sustitución molecular, permitiría descartar ya sea los procesos geológicos (ocurridos hace más de 3 millones de años) o los procesos paleoecológicos de los últimos 2 millones de años como los responsables de la estructura observada. La datación usando tasas de sustitución molecular, a pesar de ser un método limitado y a veces cuestionable, la empleo para establecer un marco temporal comparable entre las especies [25-27, 81].

Además, si estos patrones filogeográficos son producto de cambios en la distribución geográfica de las especies debidos a cambios climáticos históricos, a falta de fósiles, pueden utilizarse ENMs para hacer proyecciones geográficas sobre las condiciones climáticas del pasado, que deberían mostrar que las especies tuvieron distribuciones alopátricas congruentes con los patrones filogeográficos [82, 83]. Esto permite plantear la hipótesis que los cambios climáticos influyeron en el patrón filogeográfico de estas especies, de modo que deberían existir indicios de crecimiento poblacional, diferencias en la riqueza de haplotipos entre localidades y un alto número de haplotipos únicos que indiquen que la especie alcanzó su distribución continua actual desde uno o varios refugios [82, 84]. Esta aproximación la implemento para cuatro especies en los capítulos dos y tres [25, 27].

Finalmente, si las especies analizadas respondieron de la misma manera ante los eventos históricos que afectaron sus distribuciones en el pasado, se puede plantear la hipótesis de que existe una marcada congruencia en los patrones de variación genética entre ellas. La evaluación de esta hipótesis la hice principalmente de una manera cualitativa, ya que el muestreo no es igual para todas las especies. No obstante en el capítulo tres [25] hago una evaluación cuantitativa de esta hipótesis usando el análisis de congruencia entre matrices de distancia de dos especies que presentaron un muestreo comparable, mientras que en el capítulo cuatro [81] realizo un consenso de los patrones filogeográficos de las siete especies utilizando superárboles.

INTRODUCCIÓN (Parte 2)

Filogeografía comparada: Conceptos, métodos y patrones generales en aves neotropicales. ☼

☼ Arbeláez-Cortés, E. (2012) Filogeografía comparada: Conceptos, métodos y patrones generales en aves neotropicales. Acta Biológica Colombiana, 17, 19-38.

FILOGEOGRAFÍA COMPARADA: CONCEPTOS, MÉTODOS Y PATRONES GENERALES EN AVES NEOTROPICALES

Comparative Phylogeography: Concepts, Methods and General Patterns in Neotropical Birds

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RESUMEN

Entender los patrones y procesos de diversificación de linajes intraespecíficos en el tiempo y en el espacio es el objetivo de la filogeografía. La comparación de estos patrones filogeográficos entre especies co-distribuidas muestra indicios de la historia de una comunidad. Aquí, reviso los conceptos y la metodología de la filogeografía comparada, un campo muy activo pero con métodos de análisis heterogéneos. Para dar un marco de referencia de la filogeografía en el Neotrópico, comento los patrones filogeográficos generales de las aves de esta región. La revisión de más de 100 estudios realizados en los últimos 25 años indica que los patrones filogeográficos de cada especie a pesar de coincidir en ciertos puntos con el de otras especies co-distribuidas tienen aspectos idiosincrásicos que indican que su historia es única.

Palabras clave: aves, comunidades, filogeografia, neotrópico.

ABSTRACT

Understanding the patterns and processes involved in intraspecific lineages diversification in time and space is the aim of phylogeography. The comparison of those phylogeographic patterns among co-distributed species shows insights of a community history. Here I review the concepts and methodologies of comparative phylogeography, an active research field that has heterogeneous analytical methods. In order to present a framework for phylogeography in the Neotropics, I comment the general phylogeographic patterns of the birds from this region. This review is based on more than 100 studies conducted during the last 25 years and indicate that despite different co-distributed species seem to share some points in their phylogeographic pattern they have idiosyncratic aspects, indicating an unique history for each one.

Key words: Birds, communities, Neotropics, phylogeography.

INTRODUCCIÓN

Un resultado reiterado al estudiar la variación de caracteres en las poblaciones de una especie es que, tal variación, no es geográficamente aleatoria; sino que tiene estructura, permitiendo ver la evolución en su nivel espacial más básico (Gould y Johnston, 1972). En los estudios de filogeografía (Avise *et al*., 1987) se utilizan secuencias de ADN de varios individuos de una especie para reconstruir las relaciones históricas de sus poblaciones y luego interpretarlas geográficamente, enfatizando en la influencia de eventos geológicos o paleoecológicos que asocien la historia de esa especie con la de su ambiente (Riddle, 1996; Avise, 1998; Arbogast y Kenagy, 2001). La filogeografía, aunque con sesgo hacia los animales, ha crecido rápidamente y se ha puesto al frente de estudios microevolutivos (Avise, 2000; Soltis *et al*., 2006; Beheregaray, 2008; Hickerson *et al*., 2010) usando nuevos métodos y enfoques (Garrick *et al*., 2010; Hickerson *et al*., 2010; Chan *et al*., 2011).

La filogeografía comparada estudia los patrones filogeográficos de varias especies codistribuidas de un modo cualitativo o usando métodos explícitos, muy heterogéneos, que vale la pena revisar (*e.g.* Bermingham y Avise, 1986; Sullivan *et al*., 2000; Zink, 2002; Cartens *et al*., 2005; Lapointe y Rissler, 2005; Carnaval *et al*., 2009). El mismo término también se ha usado para denominar otro tipo de estudios que comparan los patrones filogeográficos de especies muy relacionadas pero alopátricas (*e.g.* Pastorini *et al*., 2003; Albach *et al*., 2006; Chapple *et al*., 2008) que no consideraré aquí. La filogeografía comparada ha permitido visualizar patrones y proponer procesos relacionados con el origen de la diversidad en zonas de alta riqueza de especies como el Neotrópico (Solomon *et al*., 2008; Carnaval *et al*., 2009) y en grupos taxonómicos como las aves que tiene linajes con historias naturales dispares (Burney y Brumfield, 2009; Weir, 2009). A pesar de que las aves han sido el grupo de vertebrados menos estudiado desde una perspectiva filogeográfica (Beheregaray, 2008) los patrones que han mostrado ejemplifican la ocurrencia de diversos procesos evolutivos en su historia reciente, algo muy relevante para entender la diversidad presente en zonas como el Neotrópico (*e.g*., Cadena, 2007; Milá *et al*., 2009; González *et al*., 2011). En esta revisión mis objetivos son: 1) exponer los conceptos fundamentales de la filogeografía comparada y su marco metodológico y 2) revisar el estado del conocimiento de la filogeografía de las aves Neotropicales, comentando algunos de sus patrones más generales.

MATERIALES Y MÉTODOS

Para esta revisión realicé una búsqueda del término *comparative phylogeography* en el contenido de varias revistas científicas tales como: *Molecular Phylogenetics and Evolution, Molecular Ecology, Evolution, Biological Journal of the Linnean Society y Journal of Biogeography.* Examiné los resultados de estas búsquedas, seleccionando los artículos que trataran directamente de estudios de filogeografía comparada e hice énfasis en trabajos con vertebrados terrestres. Registros adicionales fueron obtenidos de la literatura citada en estos artículos así como de búsquedas puntuales en otras revistas. Adicionalmente, con el fin de mostrar un panorama de la filogeografía de aves neotropicales, compilé todos los artículos de filogeografía que encontré para este grupo de vertebrados llevados a cabo en dicha zona, incluyendo algunos trabajos

de filogeografía comparada. El Neotrópico lo defino aquí como la mitad norte de Sur América, Centro América y la mitad sur de México y la búsqueda de trabajos la limito a especies continentales cuya distribución esté total o principalmente dentro de esta zona. Como resultado obtuve 94 artículos sobre filogeografía comparada y 30 trabajos de filogeografía en aves Neotropicales publicados durante 25 años (1986 - mayo de 2011).

FILOGEOGRAFÍA COMPARADA: FUNDAMENTOS CONCEPTUALES

De acuerdo con los artículos revisados, la filogeografía comparada busca congruencias en los patrones filogeográficos y en los procesos demográficos de especies que comparten, total o parcialmente, sus distribuciones geográficas, y contrasta tales patrones con información geográfica, paleoecológica o biogeográfica (Bermingham y Avise, 1986; Zink, 1991; Joseph *et al.*, 1995; Avise, 2000; Arbogast y Kenagy, 2001; Zink, 2002; Lapointe y Rissler, 2005; Carstens y Richards, 2007; Garrick *et al.*, 2008; Castoe *et al.*, 2009). Esta búsqueda de congruencia se fundamenta en la idea de que las especies que solapan sus distribuciones tienen una historia compartida (Bermingham y Avise, 1986; Zink, 2002; Lapointe y Rissler, 2005; Morrone, 2009). Implícita en esta interpretación está la asunción de que las especies co-distribuidas actualmente debieron estarlo también en el pasado (Carstens y Richards, 2007), por lo cual se esperaría que los mismos eventos ecológicos o geológicos hayan afectado en sincronía a esas especies, haciendo que las historias de sus poblaciones sean semejantes. Bajo este escenario, al reconstruir la historia de las especies de una región, usando métodos filogeográficos, se debería recuperar: 1) congruencia topológica, 2) congruencia temporal y 3) congruencia demográfica. A continuación comento cada uno de estos tipos de congruencia.

La congruencia topológica implica que las especies de un área geográfica respondieron concertadamente ante los mismos eventos históricos por lo que deben tener patrones filogeográficos semejantes (Sullivan *et al.*, 2000). La congruencia topológica se consideró como la hipótesis fundamental a poner a prueba en filogeografía comparada, siendo la incongruencia explicada por diferencias ecológicas entre especies (Joseph *et al.*, 1995; Turner *et al.*, 1996; Zink, 1996; Rocha *et al.*, 2002; Crawford *et al.*, 2007; Qu *et al.*, 2010). Sin embargo, varios trabajos muestran que la incongruencia topológica es frecuente (*e.g.* Turner *et al.*, 1996; Kelemen y Moritz, 1999; Rocha *et al.*, 2002; Lourie *et al.*, 2005; Roberts, 2006; Bell *et al.*, 2007; Kirchman y Franklin, 2007; Guzik *et al.*, 2009; Moussalli *et al.*, 2009; Qu *et al.*, 2010) y la evidencia paleontológica indica que las comunidades pueden variar de un modo no concertado (Bennett, 1990; Barnosky y Shabel, 2005). La interpretación de la congruencia topológica en presencia de barreras geográficas conspicuas es sencilla mientras que la incongruencia plantea el reto de identificar la razón de las diferencias entre especies. Actualmente se sabe que la incongruencia topológica puede originarse por diferencias entre especies en cuanto a: selección natural, tasas de mutación molecular, tamaño efectivo poblacional, capacidad de dispersión, diferencias sutiles entre distribuciones, factores demográficos, extinciones locales (Avise, 1998; Rocha *et al.*, 2002; Cartens *et al.*, 2005; Steele y Storfer, 2007; Garrick *et al.*, 2008) o por la aleatoriedad implícita en el proceso de coalescencia de los genes (Hugall *et al.*, 2002; Garrick *et al.*, 2008). También, se ha propuesto la idea (interesante pero poco explorada) de que la incongruencia topológica indica que no hubo

simpatría histórica entre especies (Zink, 1996, 2002). Actualmente, la dicotomía congruencia-incongruencia topológica se considera simplista, y las semejanzas en los patrones filogeográficos de especies simpátricas son vistos como puntos a lo largo de un gradiente complejo cuyos extremos son: congruencia total e incongruencia absoluta (Sullivan *et al.*, 2000; Zink, 2002; Carstens y Richards, 2007; Steele y Storfer, 2007; Garrick *et al.*, 2008), siendo el grado de congruencia un indicativo de la estabilidad histórica de la comunidad estudiada (Zink, 2002).

La congruencia temporal en la división de linajes intraespecíficos entre especies simpátricas también la estudia la filogeografía comparada y su identificación se ha potenciado con el refinamiento de métodos de dataje usando información molecular (Bermingham y Avise, 1986; Avise, 1992; Cartens *et al.*, 2005; Barber y Klicka, 2010). Su fundamento es que si dos especies comparten su patrón filogeográfico es porque un mismo evento histórico las afectó al mismo tiempo. Sin embargo, patrones filogeográficos similares pueden resultar de diferentes eventos asincrónicos (Avise, 1992; Barber *et al.*, 2006; Soltis *et al.*, 2006; Barber y Klicka, 2010); lo cual es conocido como pseudocongruencia (Soltis *et al.*, 2006). La pseudocongruencia indica que las especies pueden responder independientemente a eventos similares repetidos en un mismo lugar. Finalmente, la congruencia demográfica puede buscarse analizando indicios de cambios poblacionales históricos debidos, por ejemplo, a que varias especies aumentaron su tamaño poblacional al expandirse por una nueva área tras un cambio ambiental (Hewitt, 2000, 2001, 2004; Lessa *et al.*, 2003, 2010). Esta congruencia puede encontrarse, incluso, entre especies que no presenten estructura filogeográfica (Zink, 2002).

FILOGEOGRAFÍA COMPARADA: MÉTODOS

Tradicionalmente la identificación de congruencia en filogeografía comparada se ha hecho mediante inspección 'visual' o cualitativa de los resultados de análisis filogeográficos independientes para cada especie (Zink, 2002; Cartens *et al.*, 2005; Carstens y Richards, 2007). A pesar de ser subjetivo (Sullivan *et al.*, 2000; Soltis *et al.*, 2006), este método se encuentra tácito en casi todos los estudios de filogeografía comparada (*e.g.* Bermingham y Avise, 1986; Kelemen y Moritz, 1999; Zink *et al.*, 2001; Dawson *et al.*, 2002; Hugall *et al.*, 2002; Rocha *et al.*, 2002; Dooh *et al.*, 2006; Barber *et al.*, 2006; Roberts, 2006; Taylor y Hellberg, 2006; Bell *et al.*, 2007; Kirchman y Franklin, 2007; Crandall *et al.*, 2008; Castoe *et al.*, 2009; Guzik *et al.*, 2009; Qu *et al.*, 2010; Beatty y Provan, 2011; Oshida *et al.*, 2011; Saeki *et al.*, 2011) y solo algunos autores indican su uso (Schneider *et al.*, 1998; Sullivan *et al.*, 2000; Schäuble y Moritz, 2001). Tal vez las comparaciones 'a ojo' siguen vigentes dada la dificultad (o ¿imposibilidad?) de formalizar procesos históricos como la evolución. No obstante, existen métodos explícitos que dan rigor a la filogeografía comparada (Tabla 1). Para explicar sus generalidades agrupé estos métodos considerando el modo como usan la información filogeográfica y siguiendo el orden de ideas de Garrick *et al.* (2008). A continuación comento su uso para identificar cada tipo de congruencia en filogeografía comparada.

La congruencia topológica puede examinarse directamente usando cladogramas de áreas (Da Silva y Patton, 1993; Bermingham y Martin, 1998; Taberlet *et al.*, 1998; Schneider *et al.*, 1998; Sullivan *et al.*, 2000; Zink, 2002; Feldman y Spicer, 2006), que se generan sustituyendo las ramas terminales del cladograma de cada especie por la

Grupo de métodos	Congruencia topológica	Congruencia temporal	Congruencia demográfica	Referencias
Comparación 'directa' entre especies	Métodos biogeográficos (*e.g.* Árboles reconciliados). Pruebas de topología (*e.g.* AU)	Prueba de radio verosimilitud entre las distribuciones de tiempos calculadas para dos especies	*Sing test*	Da Silva y Patton, 1993; Bermingham y Martin, 1998; Schneider *et al.*, 1998; Taberlet *et al.*, 1998; Edwards y Beerli, 2000; Sullivan *et al.*, 2000; Zink, 2002; Smith y Farrell, 2005; Feldman y Spicer, 2006
Comparación 'indirecta' entre especies y un modelo	Pruebas de topología (*e.g.* modelos usando coalescencia)	—		Cartens *et al.*, 2005; Crawford *et al.*, 2007; Steele y Storfer, 2007; Garrick *et al.*, 2008; Solomon *et al.*, 2008
	Superárboles (*e.g.* SCAC). Mapeo de disrupciones filogeográficas	—		Turner *et al.*, 1996; Calsbeek *et al.*, 2003; Lapointe y Rissler, 2005; Rissler *et al.*, 2006; Soltis *et al.*, 2006; Victoriano *et al.*, 2008; Burney y Brumfield, 2009; Weir, 2009; Jaramillo-Correa *et al.*, 2010
'Combinación' de datos en un solo análisis	CADM	ABC	HABC	Hickerson *et al.*, 2006b; Hickerson *et al.*, 2007; Leaché *et al.*, 2007; Hickerson y Meyer, 2008; Carnaval *et al.*, 2009; Plouviez *et al.*, 2009; Barber y Klicka, 2010; Wegmann *et al.*, 2010; Roe *et al.*, 2011.

Tabla 1. Métodos explícitos usados en filogeografía comparada.

localidad/región del individuo al que corresponde. Estos cladogramas se comparan, o combinan, usando métodos biogeográficos tales como: parsimonia de Brooks (Taberlet *et al.*, 1998), análisis de componentes (Bermingham y Martin, 1998), árboles reconciliados (Bermingham y Martin, 1998), análisis de descomposición (Schneider *et al.*, 1998) o *tree mapping* (Feldman y Spicer, 2006; Sullivan *et al.*, 2000) para generar un cladograma general de áreas; que es un consenso que muestra congruencias y diferencias entre especies. Aunque explícitos, estos métodos pierden utilidad cuando hay demasiada incongruencia topológica (Sullivan *et al.*, 2000). Otra forma de 'medir' la congruencia topológica es ajustando el patrón filogeográfico de una especie en el de otra (Bermingham y Martin, 1998; Sullivan *et al.*, 2000; Steele y Storfer, 2007) con métodos estadísticos como: Kishino-Hasegawa-Templeton test (Templeton, 1983; Kishino y Hasegawa, 1989), *bootstrap* paramétrico (Efron y Tibshirani, 1993), *Shimodaira-Hasegawa test* (Shimodaira, 2002) o *approximately unbiased test* (Shimodaira y Hasegawa, 2001). Estos métodos miden diferencias de valores de 'optimalidad' entre un árbol

óptimo (generado para una especie) y un árbol ajustado a la hipótesis que se está examinando (el de otra especie) usando una distribución nula para derivar una probabilidad estadística (Sullivan *et al.*, 2000). Así se obtiene un estimador para la congruencia entre topologías junto con la probabilidad de que, este, sea mayor al esperado de comparar árboles al azar. Una aproximación similar usa el patrón de estructura genética de una especie o una estructura hipotética (ya no la topología) para evaluar los datos de otra especie, usando un análisis molecular de varianza (AMOVA), y determinar si ese agrupamiento explica bien los resultados (Schäuble y Moritz, 2001; Lourie *et al.*, 2005). Sin embargo, estos métodos solo permiten comparaciones pareadas entre especies y a pesar de haber sido usados en comunidades de vertebrados de diferentes regiones (Bermingham y Martin, 1998; Schneider *et al.*, 1998; Sullivan *et al.*, 2000; Feldman y Spicer, 2006) no han indicado congruencia topológica total.

Una manera 'indirecta' de buscar congruencia topológica es comparando los patrones filogeográficos de cada especie contra una topología hipotética (modelo); que es la esperada si las especies de un área hubieran sido afectadas por eventos históricos conocidos (Cartens *et al.*, 2005; Crawford *et al.*, 2007; Steele y Storfer, 2007; Garrick *et al.*, 2008; Solomon *et al.*, 2008). La congruencia entre los datos de cada especie y el modelo indica cuales especies se ajustan a la historia conocida del área y por lo tanto comparten sus patrones filogeográficos. Varios modelos pueden ser propuestos para representar diferentes historias (Cartens *et al.*, 2005). El ajuste de los datos al modelo se hace usando las pruebas comentadas en el párrafo anterior y otras basadas en inferencia Bayesiana (Steele y Storfer, 2007) o en coalescencia (Knowles y Maddison, 2002). Un ejemplo de esta aproximación es el de Carstens y colaboradores (Cartens *et al.*, 2005) quienes encontraron que diferentes especies en un bosque templado de Estados Unidos podían asignarse a uno de tres modelos alternativos propuestos a partir de información *ad hoc* de la historia de esa comunidad. A pesar de su utilidad estos modelos podrían sesgarse por las expectativas del investigador. Para disminuir tal sesgo se puede usar una aproximación que combina modelos de nicho ecológico (ENM) proyectados geográficamente en diferentes tiempos (condiciones paleoclimáticas) que al ser visualizados mediante sistemas de información geográfica permiten proponer modelos menos subjetivos (Chan *et al.*, 2011).

Para evitar sesgos por parte del investigador al buscar congruencia topológica también se pueden 'aglomerar', en un solo análisis, todos los patrones filogeográficos mediante un superárbol regional que sintetiza la señal filogeográfica de cada especie (Lapointe y Rissler, 2005). Si no hay congruencia topológica entre especies el superárbol no tendrá ningún patrón. Existen varios métodos para hacer superárboles (Bininda-Emonds, 2004). En filogeografía comparada se han usado tres: MRP (*matrix representation with parsimony*; Lapointe y Rissler, 2005; Victoriano *et al.*, 2008), SAC (*supertree area cladogram*) y SCAC (*sequence concatenation area cladogram*; Weir, 2009). En general se hace lo siguiente: Se diseña una matriz codificando la presencia y ausencia de los linajes de cada especie sobre una subdivisión del área de estudio (*e.g.* subregiones o una gradilla) y se analiza con parsimonia para encontrar el superárbol. También puede hacerse un superárbol (poco ortodoxo) acoplando secuencias de ADN de diferentes especies de una misma subregión y haciendo un análisis filogenético (SCAC; Weir, 2009) donde los terminales son las subregiones o los cuadros de la gradilla. Una ventaja de los superárboles es que no requieren que todas las especies sean totalmente simpátricas (Lapointe y Rissler, 2005), pero solo muestran patrones generales. Estos métodos se han implementado en regionalizaciones que buscan identificar áreas de endemismo (Weir, 2009) y zonas de 'diversificación activa' (Lapointe y Rissler, 2005) con fines de conservación. Identificar la existencia de barreras geográficas compartidas entre especies es otra manera de buscar congruencia topológica. Esto se hace identificando divisiones filogeográficas, en el espacio geográfico, para cada especie (*e.g.* SAMOVA o Barrier; Dupanloup *et al.*, 2002; Manni *et al.*, 2004) cuya superposición en un mapa muestra las zonas con divisiones compartidas (Jaramillo-Correa *et al.*, 2010). También se puede comparar el grado de diferenciación genética entre poblaciones, de

varias especies, a través de barreras geográficas predefinidas (Turner *et al.*, 1996; Burney y Brumfield, 2009; Weir, 2009) o no (Calsbeek *et al.*, 2003; Soltis *et al.*, 2006), para observar patrones compartidos. Un método reciente llamado *congruence among distance matrices* (CADM; Legendre y Lapointe 2004; Campbell *et al.*, 2011; Roe *et al.*, 2011) permite identificar congruencia global entre varias especies y, *a posteriori*, congruencia entre pares de especies usando matrices de distancia genética y de distancia geográfica al modo de un test de Mantel extendido. Otro método basado en el uso de sistemas de información geográfica permite dar mayor detalle a la representación espacial de la diferenciación genética entre localidades/poblaciones usando la superposición de 'paisajes genéticos', de especies codistribuidas, creados a partir de un algoritmo de interpolación espacial y una matriz de distancias genéticas (Vandergast *et al.*, 2010). Vale anotar que estos métodos se basan en distancias genéticas y no en patrones filogeográficos, por lo que carecen de la señal histórica que caracteriza a la filogeografía (Avise, 1992; Templeton, 1998; Avise, 2000; Templeton *et al.*, 2000). Este aspecto histórico puede integrarse poniendo en un mapa la ubicación de las divergencias topológicas más evidentes de cada especie (Rissler *et al.*, 2006).

La congruencia temporal ha sido evaluada estimando tiempos de divergencia para los linajes de cada especie y examinando, luego, si los datajes de diferentes especies están dentro de un periodo semejante (*e.g.* inicios del Pleistoceno; Schäuble y Moritz, 2001; Wares y Cunningham, 2001; Calsbeek *et al.*, 2003; Mateos, 2005; Castoe *et al.*, 2009). Como esta aproximación no tiene rigor estadístico Edwards y Beerli, 2000, propusieron usar la distribución de valores alrededor del valor máximo de verosimilitud que se obtiene usando métodos bayesianos de dataje molecular y así detectar la congruencia temporal entre especies. La comparación de estas distribuciones entre especies se hace con una prueba de radio-verosimilitud que indica si el tiempo de divergencia de las poblaciones de dos especies es significativamente diferente o no. Sin embargo, existen parámetros que varían entre las especies comparadas como son: el tamaño poblacional ancestral, la migración post-divergencia, la heterogeneidad en tasas evolutivas y la subdivisión en la población ancestral; que dan incertidumbre al dataje de divergencia reciente (Edwards y Beerli, 2000). Por esto Hickerson y colaboradores (Hickerson *et al.*, 2006a; Hickerson *et al.*, 2006b; Hickerson *et al.*, 2007) presentan un método que considera estos parámetros al poner a prueba la hipótesis de divergencia temporal simultánea entre dos poblaciones de varias especies a través de una misma barrera geográfica. El método emplea aproximate bayesian computation (ABC) y simulaciones basadas en coalescencia. Este método básicamente lo que hace es calcular hiperparámetros que describen procesos entre las especies y subparámetros que permiten que haya variación demográfica en cada especie (Hickerson *et al.*, 2006a; Hickerson *et al.*, 2006b; Hickerson *et al.*, 2007; Csilléry *et al.*, 2010). Luego simula una serie de datos bajo un modelo (*e.g.* divergencia sincrónica) usando coalescencia y permitiendo variaciones en el tamaño poblacional. Con los datos simulados calcula pseudoparámetros que reiteradamente se comparan con los parámetros de los datos reales y se aceptan o rechazar según un criterio de cercanía. Con la muestra de pseudoparámetros se construye la distribución *a posteriori* del hiperparámetro deseado que en este caso es el número de eventos de vicarianza. Lo que destaca al ABC, sobre otros métodos, es que permite el análisis de múltiples grupos de datos filogeográficos simultáneamente, considerando diferencias demográficas entre taxones (Carnaval *et al.*, 2009). Su implementación ha mostrado que entre especies afectadas por una misma barrera geográfica no ha ocurrido un único evento simultáneo de vicarianza (Hickerson *et al.*, 2006b; Leaché *et al.*, 2007; Plouviez *et al.*, 2009; Barber y Klicka, 2010; Chan *et al.*, 2011). Por último, en cuanto a la congruencia demográfica, los análisis demográficos por lo general indican crecimiento (+) o disminución (-) en el tamaño poblacional de una especie (Kuhner, 2008), de modo que cualquier sesgo significativo hacia una de las dos posibilidades indicaría congruencia demográfica entre especies. La identificación de un sesgo crecimiento/disminución puede hacerse usando el *sign test*, una prueba sencilla comparable a las tablas de contingencia (Smith y Farrell, 2005). Otro modo de poner a prueba hipótesis explicitas que involucran aspectos demográficos entre especies es usar *hierarchical approximate bayesian computation* (HABC) un método similar al ABC, que puede integrar múltiples parámetros (*e.g.* migración) para crear modelos evolutivos más flexibles (Hickerson y Meyer, 2008; Carnaval *et al.*, 2009; Chan *et al.*, 2011). Aunque la congruencia demográfica es la menos estudiada en filogeografía comparada,

su detección ha indicado procesos que han afectado comunidades enteras (Wares y Cunningham, 2001; Lessa *et al.*, 2003; Smith y Farrell, 2005; Crandall *et al.*, 2008; Garrick *et al.*, 2008; Lessa *et al.*, 2010). La identificación de esta congruencia en combinación con otros métodos fue parte de un elegante estudio con fines de conservación en el bosque Atlántico brasilero (Carnaval *et al.*, 2009).

Generalidades del diseño de los estudios de filogeografía comparada

Vale la pena decir que uno o varios de estos métodos los encontré implementados en solo el 20% de los trabajos de filogeografía comparada que revisé (n = 94). A pesar de que la filogeografía comparada aun tiene un sesgo hacia lo descriptivo los problemas que ha abordado son variados. Los estudios se han realizado con: entre una especie (contraintuitivo, pero es el caso de una especie de salmón con poblaciones simpátricas alocrónicas; Churikov y Gharrett, 2002) y 55 especies (Calsbeek *et al.*, 2003) en el caso de revisiones de varios trabajos para una región, siendo incluidas en la mayoría de estudios entre dos y cuatro especies. Llama la atención que estos trabajos han incluido desde especies muy relacionadas filogenéticamente (Turner *et al.*, 1996; Dawson *et al.*, 2002; Feldman y Spicer, 2006) hasta taxones muy diferentes (Taberlet *et al.*, 1998; Calsbeek *et al.*, 2003; Cartens *et al.*, 2005). En cada extremo de esta disparidad taxonómica los autores argumentan diferente, diciendo que en los estudios de filogeografía comparada hay que limitar taxonómica y ecológicamente las especies estudiadas para poder encontrar patrones compartidos (Feldman y Spicer, 2006) o que mientras más disparidad exista las congruencias encontradas tendrán mayor significado (Taberlet *et al.*, 1998; Cartens *et al.*, 2005). Geográficamente, los estudios van desde locales (Garrick *et al.*, 2008; Guzik *et al.*, 2009) hasta continentales (Zink, 1996; Joseph y Wilke, 2007; Weir, 2009). También hay trabajos estudiando interacciones ecológicas marcadas que a pesar de ser ejemplos de coevolución no han mostrado la congruencia filogeográfica esperada entre esas especies (*e.g.* Parker *et al.*, 2004; Richards *et al.*, 2007; Roe *et al.*, 2011). A pesar de que las secuencias de ADN han sido la fuente principal de datos, se han incluido también otros marcadores moleculares como AFLPs y microsatélites como parte de la filogeografía comparada (*e.g.* Calsbeek *et al.*, 2003; Guzik *et al.*, 2009; Maliouchenko *et al.*, 2007), haciendo posible una aproximación integrativa a varios 'niveles temporales' (Garrick *et al.*, 2008; Garrick *et al.*, 2010; Wegmann *et al.*, 2010). Adicionalmente, éstos estudios se han complementado usando reconstrucciones paleoecológicas, principalmente modelos de nicho ecológico proyectados en condiciones ambientales del pasado (Joseph *et al.*, 1995; Hugall *et al.*, 2002; Bell *et al.*, 2007; Carstens y Richards, 2007; Solomon *et al.*, 2008; Carnaval *et al.*, 2009; Moussalli *et al.*, 2009; Beatty y Provan, 2011), aunque es necesario indicar que existen limitaciones de esta última aproximación (Nogués-Bravo, 2009).

Filogeografía de aves neotropicales: un ejemplo de patrones generales en la historia de una biota diversa

A pesar de que encontré 30 estudios filogeográficos que incluyen 29 especies pertenecientes a diez familias y cinco órdenes de aves (Brawn *et al.*, 1996; Marks *et al.*, 2002; González *et al.*, 2003; García-Moreno *et al.*, 2004; Lovette, 2004; Solórzano *et al.*, 2004; Cheviron *et al.*, 2005; Aleixo, 2006; Cabanne *et al.*, 2007; Cadena *et al.*, 2007; Chaves *et al.*, 2007; Nyari, 2007; Bonaccorso *et al.*, 2008; Cabanne *et al.*, 2008; Cortés-Rodríguez *et al.*, 2008a,b; Miller *et al.*, 2008; Navarro-Sigüenza *et al.*, 2008; Puebla-Olivares *et al.*, 2008; Weir *et al.*, 2008; Caparroz *et al.*, 2009a; Caparroz *et al.*, 2009b;

Milá *et al.*, 2009; Sanín *et al.*, 2009; Vázquez-Miranda *et al.*, 2009; Arbeláez-Cortés *et al.*, 2010; Pérez-Emán *et al.*, 2010; Cadena *et al.*, 2011; D'Horta *et al.*, 2011; González *et al.*, 2011), en la mayoría de casos la distribución de estas especies no coincide, impidiendo hacer un análisis filogeográfico comparativo de todas ellas. No obstante existen cinco estudios comparativos (Bates *et al.*, 2003; Bates *et al.*, 2004; Burney y Brumfield, 2009; Weir, 2009; Barber y Klicka, 2010) que incluyen especies adicionales pero aunque su muestreo no es intensivo (ver más adelante) si abordan de manera explícita la filogeografía comparada de las aves. Por consiguiente, me limitaré a comentar cualitativamente estos trabajos y a presentar algunos de los patrones filogeográficos generales que parecen emerger para la avifauna Neotropical.

En estos estudios el número de individuos incluidos varía entre 21 y 160. Todos los estudios han usado secuencias de ADNmt, y únicamente dos incluyeron también secuencias nucleares (Cabanne *et al.*, 2008; D'Horta *et al.*, 2011) y tres usaron otros marcadores moleculares además de secuencias de ADN (Caparroz *et al.*, 2009a; Milá *et al.*, 2009; González *et al.*, 2011). La escala geográfica va de regional (González *et al.*, 2003; Chaves *et al.*, 2007; Milá *et al.*, 2009) a continental (Marks *et al.*, 2002; Cheviron *et al.*, 2005; Cadena *et al.*, 2007; Nyari, 2007; Weir, 2009). Aquí consideraré las especies como de montaña (>1500 m) o de tierras bajas (<1500 m). Estos ecosistemas, aunque comparten grupos taxonómicos, representan dos tipos de avifaunas con aspectos ecológicos y evolutivos diferentes (Weir, 2006; Cadena *et al.*, 2007).

Algunos estudios de filogeografía de aves Neotropicales incluyen dataje molecular (García-Moreno *et al.*, 2004; Lovette, 2004; Cheviron *et al.*, 2005; Chaves *et al.*, 2007; Miller *et al.*, 2008; Weir *et al.*, 2008; Caparroz *et al.*, 2009a; Caparroz *et al.*, 2009b; D'Horta *et al.*, 2011; González *et al.*, 2011) que indican que los linajes intraespecíficos de estas especies se originaron hace entre cinco millones de años y 40.000 años, siendo la mayoría originados durante los últimos dos millones de años. Teniendo en cuenta las diferencias entre los métodos usados, los datos parecen señalar que los linajes filogeográficos de aves Neotropicales se originaron entre el Plioceno y el Pleistoceno. Precisamente el proceso histórico más comúnmente considerado para explicar los patrones filogeográficos han sido las fluctuaciones climáticas del Cuaternario (García-Moreno *et al.*, 2004; Aleixo, 2006; Chaves *et al.*, 2007; Cabanne *et al.*, 2008; Miller *et al.*, 2008; Caparroz *et al.*, 2009b; Arbeláez-Cortés *et al.*, 2010; Pérez-Emán *et al.*, 2010; D'Horta *et al.*, 2011; González *et al.*, 2011) que han hecho que los hábitats, montanos y de tierras bajas, se fragmenten y promuevan la diferenciación genética entre poblaciones alopátricas. Para especies de tierras bajas la formación de grandes ríos en Sur América (Marks *et al.*, 2002; Bates *et al.*, 2003; Bates *et al.*, 2004; Cheviron *et al.*, 2005; Nyari, 2007; Cabanne *et al.*, 2008) y de cadenas montañosas (Lovette, 2004; Cheviron *et al.*, 2005; Chaves *et al.*, 2007; Milá *et al.*, 2009) así como incursiones marinas (Brawn *et al.*, 1996; González *et al.*, 2003; Lovette, 2004) también se han considerado como modeladores de su estructura filogeográfica. No obstante, estos procesos no actuaron independientemente pero su efecto es difícil de separar (Cheviron *et al.*, 2005; Cabanne *et al.*, 2007, 2008). Adicionalmente, estudios que incluyen datos fenotípicos y ambientales así como información de otros marcadores moleculares han permitido identificar otros procesos, como selección natural o diferencias en flujo génico entre machos y hembras (Chaves *et al.*, 2007; Caparroz *et al.*, 2009a; Milá *et al.*, 2009; González *et al.*, 2011) como parte de la historia de estas aves. Finalmente, hay evidencia de crecimiento demográfico reciente de varias especies de aves (Cheviron *et al.*, 2005; Aleixo, 2006; Cabanne *et al.*, 2008; Cortes-Rodríguez *et al.*, 2008; Caparroz *et al.*, 2009b; Pérez-Emán *et al.*, 2010) que es interpretado como una respuesta a cambios ambientales 'favorables'. También se han señalado los Andes (Cheviron *et al.*, 2005; Miller *et al.*, 2008; Milá *et al.*, 2009), y las tierras bajas del Istmo de Tehuantepec (Cadena *et al.*, 2007; Cortés-Rodríguez *et al.*, 2008; Pérez-Emán *et al.*, 2010) como barreras para especies de tierras bajas y montanas, respectivamente. No obstante el efecto de esas barreras no ha sido igual para todas las especies (Marks *et al.*, 2002; Miller *et al.*, 2008; Arbeláez-Cortés *et al.*, 2010).

Algunas de las especies estudiadas tienen distribuciones geográficas compartidas que permiten comparar sus patrones filogeográficos con detalle. Por ejemplo, hay tres especies de montaña, con datos filogeográficos para México y Centro América. Estas especies son: *Arremon brunneinucha* (Cadena *et al.*, 2007; Navarro-Sigüenza *et al.*, 2008), *Chlorospingus ophthalmicus* (García-Moreno *et al.*, 2004; Bonaccorso *et al.*, 2008; Weir *et al.*, 2008) y *Lepidocolaptes affinis* (Arbeláez-Cortés *et al.*, 2010); y a pesar de ser simpátricas su congruencia topológica es poca. Solo ciertos detalles, para México, como el aislamiento del macizo de los Tuxtlas y del norte de la sierra Madre del Sur coinciden, pero la diferenciación de la sierra Madre Oriental observada en *A. brunneinucha* y *C. ophthalmicus* no es evidente en *L. affinis*. Para Centro América el istmo de Tehuantepec es importante en la diferenciación de *A. brunneinucha* y *C. ophthalmicus*, pero para *L. affinis* la depresión de Nicaragua es la barrera más clara. Estos resultados son esperados por diferentes razones, según discutí al principio. No obstante en este caso la falta de congruencia topológica podría deberse a un factor que no se ha considerado previamente, y es que las unidades taxonómicas no son comparables, por ejemplo como resultado de estos análisis *A. brunneinucha* y *C. ophthalmicus* parecen representan más de una especie (*e.g.*, García-Moreno *et al.*, 2004; Cadena *et al.*, 2007).

Finalmente, existen al menos cinco estudios de filogeografía comparada de aves Neotropicales que examinan los niveles de diferenciación genética entre poblaciones (Bates *et al.*, 2004; Bates *et al.*, 2003; Burney y Brumfield, 2009; Weir, 2009, Barber y Klicka, 2010); aunque en tres de ellos no se ponen a prueba hipótesis de congruencia entre especies. Estos estudios encontraron que, para las especies de montaña, las tierras bajas (*e.g.* valle del río Marañón en Perú e istmo de Tehuantepec en México; Weir, 2009; Barber y Klicka, 2010) afectan su patrón filogeográfico pero que no necesariamente la vicarianza a través de estas barreras fue sincrónica. Para aves de tierras bajas se encontró que las diferencias genéticas a través de cadenas montañosas y de ríos se relacionan bastante con la ecología de las especies, siendo las aves de dosel las que presentan menor diferenciación (Burney y Brumfield, 2009). Para especies de zonas menos boscosas (*e.g.* el cerrado entre Brasil y Bolivia) se encontró poca diferenciación genética, a pesar de una gran separación geográfica, que es atribuida a alto flujo génico o a una expansión poblacional reciente (Bates *et al.*, 2003). Aunque patrones filogeográficos compartidos como estos empiezan a emerger para las aves Neotropicales; la representación en estos trabajos de grupos diversos y representativos del Neotrópico, como por ejemplo las tangaras (familia Thraupidae), es prácticamente nula. Por lo tanto los patrones filogeográficos que están emergiendo podrían no ser generales.

CONCLUSIÓN

La filogeografía comparada se ha establecido como uno de los campos más activos de investigación en evolución reciente de las biotas. A pesar de que sus conclusiones se han basado principalmente en comparaciones cualitativas existe ahora un grupo de métodos que permiten poner a prueba, explícitamente, hipótesis sobre la historia compartida de especies simpátricas. Los estudios filogeográficos de la avifauna Neotropical empiezan a mostrar patrones compartidos entre especies. Sin embargo el número de estos trabajos es muy bajo en comparación con la diversidad de esta región. La combinación de diferentes métodos e información, dentro del marco de la filogeografía comparada, resultará en un entendimiento detallado de la historia de las comunidades permitiendo conocer aspectos relacionados con su estabilidad y con su respuesta a cambios ambientales o procesos históricos que han dejado indicios en el patrón filogeográfico de sus especies.

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CAPÍTULO 1

Molecular evidence of the taxonomic status of western Mexican populations of *Phaethornis longirostris* (Aves: Trochilidae)☼

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Molecular evidence of the taxonomic status of western Mexican populations of *Phaethornis longirostris* (Aves: Trochilidae)

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Abstract

Species diversity is largely underestimated by current taxonomy, precluding a precise understanding of evolutionary processes. Genetic data have increased our understanding of that cryptic diversity, and multilocus studies are now desirable. In this study, we used mitochondrial and nuclear DNA sequences to evaluate the taxonomic status of the western Mexico's populations of *Phaethornis longirostris*. We found differences of 4.2 % in mtDNA and different alleles for one nDNA locus between western and eastern Mexican populations. Molecular and morphological evidence support the separation of these populations (*P. l. mexicanus* and *P. l. griseoventer*) as the species *Phaethornis mexicanus* Hartert 1897. *Phaethornis mexicanus* is endemic to western Mexico and sister to the remaining populations of *P. longirostris*. The speciation of *P. mexicanus* probably occurred around 880,000 years ago by a vicariant event involving climatic-vegetational changes.

Key words: Hummingbirds, Mesoamerica, niche conservatism, speciation, species limits, tropical dry forest

Introduction

The Neotropics host the world's most diverse avifauna (Newton 2003), but their species richness is largely underestimated by current taxonomy (Navarro-Sigüenza & Peterson 2004; Peterson & Navarro-Sigüenza 2009; Tavares et al. 2011; Milá et al. 2012). For Mesoamerica (i.e., Mexico and Central America), several phylogenetic and phylogeographic studies of birds have indicated marked genetic differentiation of allopatric populations that also show morphological differences or are isolated by geographic barriers (e.g., Navarro-Sigüenza et al. 2008; Weir et al. 2008; Arbeláez-Cortés et al. 2010; Barber & Klicka 2010; Bonaccorso et al. 2011; González et al. 2011; Arbeláez-Cortés et al. 2012). Those studies have been mainly based on information from mitochondrial DNA (mtDNA), but it is now possible and desirable to add nuclear DNA (nDNA) loci to facilitate the detection of patterns derived from species-level processes rather than from single locus histories (Backström et al. 2008; Edwards & Bensch 2009). The combination of molecular information, phenotypic traits, and ecological data can be instrumental in recognizing species-level cryptic diversity (Padial et al. 2010; Milá et al. 2012). Moreover, the recognition of an appropriate taxonomic rank for a particular lineage has consequences both for conservation purposes (Peterson & Navarro-Sigüenza 1999; Rojas-Soto et al. 2009) and for the understanding of evolutionary processes.

The hummingbirds (Aves: Trochilidae) are endemic to the Americas and comprise 342 species (Gill & Donsker 2013). The hermits (subfamily Phaethorninae) are both phylogenetically and morphologically well differentiated from the remaining species (Hinkelmann 1996; Hinkelmann & Schuchmann 1997; Stiles 2004; McGuire et al. 2007). Hermits are relatively dull-colored with little or no brilliant iridescence, are non-territorial trap-liners, and are lekking species (Hinkelmann 1996; Stiles 2004). This group, which is restricted to Neotropics, contains 35 species in six genera; 26 of these are in the genus *Phaethornis* (Gill & Donsker 2013).

Phaethornis longirostris (De Lattre 1843), a widespread species ranging from western Mexico to northwestern Peru, comprises six subspecies. This taxon was considered as part of the long-tailed hermit (*P. superciliosus*) until the morphological works of Hinkelmann (1996) and Hinkelmann & Schuchmann (1997), who recognized all populations west of the Andes north to Mexico as the species *P. longirostris*. Western Mexican populations became the subspecies *P. l. mexicanus* (Guerrero-Oaxaca, Hartert 1897) and *P. l. griseoventer* (Nayarit-Colima, Phillips 1961), which inhabit the endangered Neotropical dry forest and submontane forests of western Mexico, and are isolated from the remaining Mexican populations of *P. longirostris* by the Sierra Madre del Sur and Sierra Madre Occidental (Hinkelmann 1996; Gill & Donsker 2013). It has been suggested that these populations are adapted to less humid forest types than the remaining subspecies of *P. longirostris*, except *P. l. baroni* from western Ecuador (Hinkelmann 1996), which also occurs in a similar 'drier' ecosystem. Populations of *P. longirostris* in western Mexico and western Ecuador were originally described as species (*P. mexicanus* and *P. baroni*, Hartert 1897), and the former has been recognized by some recent taxonomic authorities (e.g., Howell & Webb 1995; Gill & Wright 2006; Howell 2013). Other authors have considered each of the two western Mexican subspecies as species (Hinkelmann 1996; Navarro-Sigüenza & Peterson 2004). However, no molecular phylogenetic analysis has been undertaken to clarify the taxonomic status of those populations.

In this study, we used a multilocus dataset to evaluate the taxonomic status of western Mexican populations of *P. longirostris* and to estimate a date for the differentiation of the Mexican populations. We also analyze morphologically diagnostic characters and test the hypothesis of niche conservatism to gain insight into the process involved in their differentiation.

Methods

Sampling and laboratory procedures. Tissue and skin samples from voucher specimens were obtained from the bird collection at the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC) (see Appendix). DNA was isolated from tissues by a standard high-salt and chloroform:isoamyl alcohol method, and from small pieces of skin of recent museum specimens (rinsed with ethanol for 24 h) using Qiagen DNeasy™ kit (Qiagen Inc., Valencia, CA, USA) with the following modifications: 7µL of 1M dithiothreitol were added to the ATL buffer, and the AE buffer was diluted 1:10 and preheated to 70°C, then used to eluted DNA in 20- 50 mL. DNA isolations from skins included a negative control and were visualized in agarose gels stained with ethidium-bromide, and we never observed a band for the controls. Moreover, we performed isolations from skins mainly to obtain sequences from *P. l. griseoventer*. DNA from two tissue samples of this subspecies was isolated after obtaining the sequences of the skin samples, avoiding contamination of the skin samples with DNA from fresh tissue.

We obtained both maternally inherited mtDNA and bi-parentally inherited nDNA sequences for 26 samples of *Phaethornis* from Mexico (see Appendix). The mitochondrial gene ND2 (subunit 2 nicotinamide adenine dinucleotide dehydrogenase) was amplified by PCR using primers H6313 and L5216 or L5219 (Sorenson et al. 1999) and, for the skin samples, using internal primers specifically designed for this study (EAC-ND2Lint3 5'CCCACCCTACTTACTATAATAGC3' and EAC-ND2HIn1 5'GAGATDGADGAGAAGGCTA3'). The mitochondrial gene COI (cytochrome c oxidase subunit 1) was amplified using primers COIBirdF1 and COIBirdR2 (Hebert et al. 2004). In addition, we amplified and sequenced the following nDNA loci: locus 20454, using primers 20454F and 20454R (Backström et al. 2008), and intron 11 of GAPDH (glyceraldehyde-3-phosphate dehydrogenase), using primers GapdL890 and GapdH950 (Friesen et al. 1997). Volume for all PCRs was 15µL, including 1x PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM each dNTP, 0.4-0.5 µM each primer, 1-2 unit DNA polymerase, and ca. 50–100 ng of DNA.

The PCR protocol for ND2 and COI was 10 cycles of 94°C for 15 s, 55°C for 30 s, 72°C for 30 s; followed by 35 cycles of 94°C for 15 s, 50°C for 30 s, 72°C for 30 s; and a final extension at 72°C for 7 min. The protocol for ND2 fragments amplified using the internal primers was 5 cycles of 95°C for 30 s, 59 or 58°C for 30 s, 72°C for 1 min; followed by 5 cycles of 95°C for 15 s, 57 or 54°C for 30 s, 72°C for 1 min; followed by 35 cycles of 94°C for 15 s, 51°C for 30 s, 72°C for 30 s; and a final extension at 72°C for 7 min. The protocol for the 20454 locus was 20 cycles of 95°C for 30 s, 65 to 55°C for 1 min (decreasing temperature with 1°C each two cycles), 72°C for 1 min; followed by 20 cycles of 95°C for 30 s, 55°C for 30 s, 72°C for 1 min; and a final extension of 72°C for 5 min. We also used a different touch-down protocol, decreasing annealing temperature from 52°C to 46°C each five cycles, for amplifying this locus in some samples. GAPDH was amplified using 35 cycles of 94°C for 1 min, 57°C for 45 s, and 72°C for 1 min, and a final extension of 72°C for 10 min. PCR products were purified using Exo-SAP-IT™ (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA). The sequences were obtained using ABI Prism Bigdye™ v3.1 (Qiagen Inc., Valencia, CA, USA) terminator chemistry in an ABI 3730XL automated

sequencer. Sequences were edited and aligned manually using BioEdit (Hall 1999), and scanned across all individuals to check for accuracy and consistency. For nDNA sequences, we inspected chromatograms to detect double peaks, which were coded using standard IUPAC ambiguity codes. The allele phase of each nDNA locus was resolved using the coalescent-based Bayesian method of the Phase algorithm (Stephens et al. 2001; Stephens & Donnelly 2003) in DnaSP v.5 (Librado & Rozas 2009) employing 10,000 iterations, 10 thinning intervals, 1000 burn-in, allowing for recombination, and setting an output probability threshold of 0.9. We used the resulting highest-probability haplotypes for further analyses. All sequences are deposited in GenBank (KF525853–KF525939).

Phylogenetic pattern and divergence time analyses. We constructed two ND2 datasets because of difficulty in obtaining complete sequences for some samples. First, we constructed a 980 bp matrix that included new sequences of 14 individuals of *P. longirostris* from Mexico; 55 sequences of additional individuals of *P. longirostris* from Mexico, Belize, Honduras, Panama, and Ecuador, obtained from the GenBank; and sequences of 15 other species of *Phaethornis* and the outgroup species *Glaucis aeneus*, also from GenBank (Altshuler et al. 2004; McGuire et al. 2007; Graham et al. 2009; Miller et al. 2010; Naka et al. 2012). We included only those GenBank sequences for which geographic origin of the voucher was known. Second, we constructed a matrix of 463 bp for the ND2 that included additional new sequences of eight Mexican individuals.

We used Bayesian Inference (BI) and Maximum Parsimony (MP) to reconstruct phylogenetic relationships based on the ND2 980 bp dataset. BI was implemented using MrBayes 3.1 (Ronquist & Huelsenbeck 2003) with two parallel runs, one 'cold' and three 'hot' chains for 20 million generations, sampling every 2000 generations. Data were analyzed under the best-fit model selected using Akaike's information criterion in MrModeltest (Nylander 2004). A 25 % burn-in was used, and a majority rule consensus tree was calculated. The MP analysis was conducted in WinClada (Nixon 2002) using a heuristic search under the following conditions: TBR, 50,000 replicates, 5000 start points, and 250,000 trees in memory. Clade support was assigned using 100 bootstrap replicates, each with 1000 search repetitions and 100 random starting trees. We used Mega 5.2 (Tamura et al. 2011) to quantify genetic distances (K2P) among some related species of *Phaethornis* to compare with the differences between the two Mexican populations of *P. longirostris*. Network 4.6 (Bandelt et al. 1999) was used to construct haplotype and allele networks for Mexican populations of *P. longirostris* using the median-joining algorithm for each locus (ND2 463 bp, COI, GAPDH, and 20454).

We used *BEAST (Heled & Drummond 2010) in BEAST 1.7.4 (Drummond et al. 2012) to calculate divergence time between the two western subspecies and the eastern Mexican population. The *BEAST dataset included ND2 (463 bp), COI (438 bp), 20454 (371 bp), and GAPDH (372 bp). We ran *BEAST for 200 million steps, sampling every 2000 steps, using a Yule speciation tree prior, a UPGMA starting tree, a log normal relaxed uncorrelated molecular clock, and mutation rates of 2.9×10^{-8} substitutions/site/year for ND2, 1.6×10^{-8} substitutions/site/year for COI, 1.2×10^{-9} substitutions/site/year for GAPDH, and 1.67×10^{-9} substitutions/site/year for 20454, according to rates reported previously for those, or similar, markers in birds (Weir & Schluter 2008; Lerner et al. 2011; Lim & Sheldon 2011). After the analysis, we used TreeAnnotator 1.7.4 (Rambaut & Drummond 2012) to generate a tree-file compiling the data, using a 25 % burn-in and a posterior probability limit of 0.5. We also used Tracer 1.5 (Rambaut & Drummond 2009) to determine that our sampling of the posterior distribution had reached a sufficient effective sample size (ESS) and to ascertain that the number of generations required to reach stationarity of the posterior distribution had been reached. Trees obtained in the *BEAST search were visualized using DensiTree 2.01 (Bouckaert 2010) which allows a visual representation of multiple trees and identification of points of agreement regarding the topology and branch lengths. We calculated F_{ST} in DnaSP 5 (Librado & Rozas 2009) for each locus among the three taxa that occur in Mexico.

Morphological variation. We measured standard morphological traits (i.e., bill depth and bill width at the distal point of the nostril operculum, exposed culmen length, tail length, and wing chord) of all specimens of *P. longirostris* housed at MZFC, UNAM (n = 93 individuals), with a Mitutoyo Absolute Digimatic caliper (to the nearest 0.01 mm). We conducted a Principal Components Analysis (PCA) in PAST (Hammer et al. 2001), including only individuals for which all measures were available (n = 82), to test whether morphometric variation clusters individuals by geography.

Considering the molecular information (Fig. 1), we divided the series of 93 individuals from the MZFC in two groups: 1) eastern Mexico (n = 28) and 2) western Mexico (n = 65). Based on Hartert (1897) and information from other morphological works (Hinkelmann 1996; Hinkelmann & Schuchmann 1997), we examined the outer rectrices of all specimens to determine whether they were tipped only with white. Tail length measurements, which were identified as the major trait involved in size variation (see below) were also compared between eastern and western Mexico populations, using a Mann-Whitney test.

Test of environmental niche divergence. Primary geographic records for museum vouchers were obtained from various sources (BioMap Project / Darwin Database 2003; Navarro et al. 2003; Global Biodiversity Information Facility 2012). Geographic coordinates were taken either from the primary sources, when available, or from gazetteers (Paynter 1993, 1997; GeoNames 2013). We compiled 77 unique localities for vouchers from western Mexico and 234 for the remaining *P. longirostris*. To obtain the environmental niche models (ENM) necessary for comparisons in ENMtools (Warren et al. 2008, 2010) we used 13 bioclimatic variables from WorldClim (Hijmans et al. 2005), including only variables that were not highly correlated (pairwise r <0.9 considering all sample locations).

To evaluate niche differentiation between the western Mexican populations and the remaining *P. longirostris* populations that belong to different clades (Fig. 1), we used the background test in ENMTools 2.1 with 100 replicates (Warren et al. 2008, 2010). This test evaluates whether the environmental niche models obtained from two allopatrically distributed populations are more different than would be expected given the underlying environmental differences between the regions in which they occur (i.e. background; Warren et al. 2008, 2010). We defined the background for each major clade as polygons drawn along the external occurrence points plus a 25 km buffer. The background test generates a null distribution for niche differences (I values) expected between one species and occurrence points placed at random within the background of the other species (Warren et al. 2010). The I value ranges from 0, when species predicted environmental tolerances do not overlap, to 1, when all grid cells are estimated to be equally suitable for both species (Warren et al. 2010). The 100 null I values were summarized in frequency histograms and compared with the observed I value between the two clades. We used Maxent 3.3 (Phillips et al. 2006) to generate ten ENMs for each clade, and choose the model with the higher value for the statistic Receiver Operating Characteristic Area Under the Curve. Those best-models were then used to calculate the observed I value between the clades. Additionally, we used the ENMs geographic projections to identify areas where climatic conditions are suitable for each clade and contrasted them with the expectations of speciation driven either by niche conservatism or by niche differentiation (see Kozak & Wiens 2006).

Results

Both BI and MP phylogenetic reconstructions agree in topology, they indicated that *P. longirostris* is monophyletic with high support (Fig. 1). The *P. longirostris* clade is sister to another that includes *P. guy,* a Central-South American species, and the completely South American *P. superciliosus*, *P. malaris*, and *P. yaruqui*. *Phaethornis longirostris* was divided into two major clades. One included all *P. longirostris* individuals from Ecuador, Central America, and Eastern Mexico. Another clade comprised only western Mexican individuals. The haplotype network constructed using the 406 bp ND2 dataset also showed that eastern Mexican individuals are separated from those from western Mexico by 17 mutations (4.2 % of the sequence analyzed, Fig. 2). The two western Mexico subspecies were separated by two mutations (0.5 %). K2P distances between western Mexico populations and the remaining *P. longirostris* were larger (mean = 0.048) than distances found herein between other fully recognized species pairs such as *P. ruber* - *P. atrimentalis* (0.027), *P. petrei* - *P. augusti* (0.031), and *P. bourcieri* - *P. hispidus* (0.002). The division between eastern and western Mexican populations was also supported by 14 mutations in the COI dataset, whereas the two western Mexico subspecies where separated by just one mutation in this marker (Fig. 2). The nDNA locus 20454 also supported the division observed in the mtDNA; almost all western Mexican samples shared an allele that differed from the eastern Mexico allele (Fig. 2). Finally, the GAPDH presented five alleles, the most common being shared by all Mexican populations (Fig. 2). However, two GAPDH alleles were found only in the western Mexican populations and other two only in the eastern Mexican populations, indicating some genetic structure in this locus. The F_{ST} values between each pair of Mexican subspecies (Table 1) showed the same pattern depicted by the networks: a clear division between eastern and western populations in three loci, and some degree of structure in *P. l. mexicanus* and *P. l. griseoventer* only in the mtDNA.

TABLE 1. F_{ST} values for each Mexican *P. longirostris* taxon pair and for each locus.

Taxon A	Taxon B	F_{ST} ND2	F_{ST} COI	F_{ST} 20454	F_{ST} GAPDH
P. l mexicanus	*P. l. griseoventer*	0.8	0.75	0	0
P. l. mexicanus	*P. l. longirostris*	0.9	0.97	0.98	0.18
P. l. griseoventer	*P. l. longirostris*	0.9	0.99	1	0.16

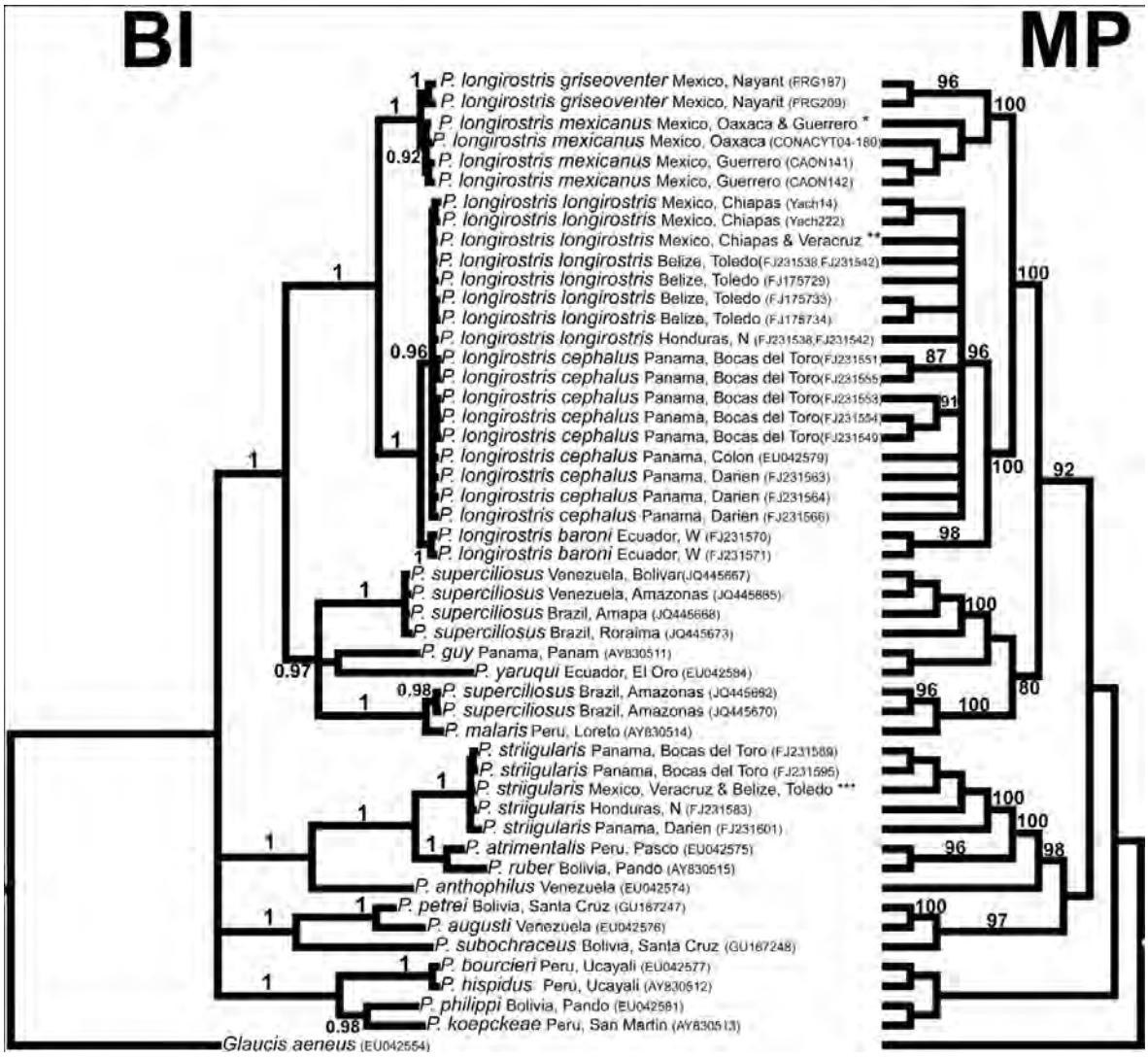

FIGURE 1. Phylogenetic results. Bayesian Inference (left) and Maximum Parsimony (right) phylogenetic reconstructions of the relationships among *Phaethornis* haplotypes based on sequences of the mitochondrial gene ND2. The a posteriori support (BI) and bootstrap support (MP) is depicted at each node. Field number is indicated for each sample sequenced for this study, and GenBank accession numbers are indicated for the remaining samples. Multiple samples with the same haplotype are not shown but are instead indicated by asterisks as follows:* = SRSC91, PLU248, PLU290, PLU315, CONACYT04-221; ** = Yach306, Yach382, FJ231527, FJ231528, FJ231529, FJ231530, FJ231531, FJ231533, FJ231534, FJ231536;*** = FJ175755, FJ231576, FJ231577, FJ231578, FJ231579, FJ231580.

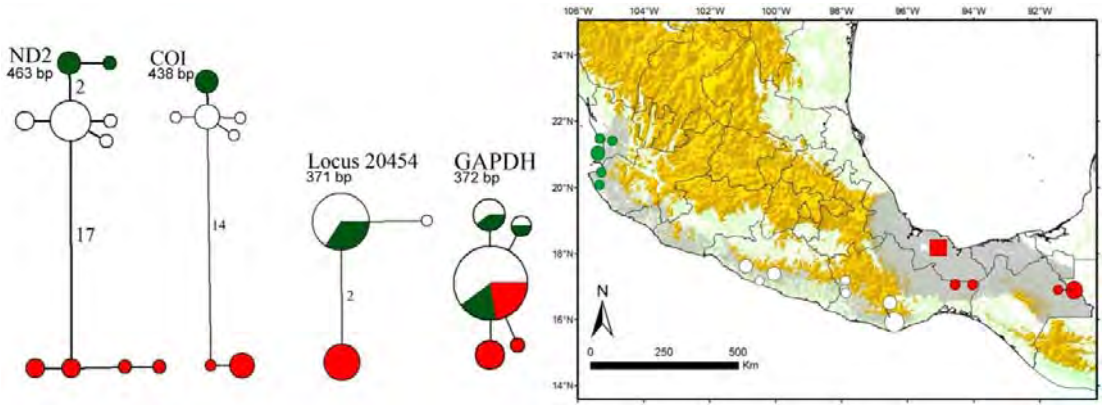

FIGURE 2. Haplotype and allele networks for each mtDNA and nDNA marker of the Mexican samples. The map depicts in gray the range of *P. longirostris* 'sensu lato' in Mexico; highlands are depicted in yellow. Color points indicate the sample localities and correspond to the colors in the networks. The square indicates samples obtained from the GenBank.

The species tree analysis in *BEAST (ESS = 296) set a time frame (Fig. 3A) for the occurrence of the division between western and eastern Mexico populations at 880,000 years ago (95% High Posterior Density from 460,000 to 1,360,000 years ago), while the division of the two western Mexico subspecies was estimated at 43,000 years ago (95% HPD from 10,000 to 97,000 years ago). The densitree (Fig. 3B) indicated agreement of the branch lengths of different trees depicting a close relationship between the two western Mexico taxa.

Principal components 1 and 2 explained the majority of size variation in morphological measurements, 90 % and 7 % respectively. PC 1 was highly and positively correlated with tail length (r = 0.93), whereas PC 2 was positively correlated with exposed culmen and wind chord (r = 0.66). The PCA scatter plot (Fig. 4A) showed a clear division between individuals from western and eastern Mexico, indicating that western Mexican individuals are larger, particularly in tail length. Only one individual from eastern Mexico (Los Tuxtlas region, Veracruz) approached the values for individuals from western Mexico (Fig. 4A). Morphometric measurements did not indicate differences between *P. l. griseoventer* and *P. l. mexicanus*. Tail lengths were different and non-overlapping (Mann-Whitney U = 0, $p < 0.001$) between eastern Mexico (mean = 70.94 mm; range = 62.8–79.5 mm; n = 25) and western Mexico populations (mean = 84.42 mm, range = 80–89.7 mm; n = 60). Additionally, all 65 specimens from western Mexico presented outer rectrices tipped only with white; whereas 26 of 28 eastern Mexico individuals presented different degrees of rusty buff. Tail feathers of the two eastern Mexico individuals that lacked rusty buff coloration were worn. The rusty color in some cases comprises only a small area in the border of the feather (see Fig. 4B), and may have been absent on these two individuals due to the feather wear.

Analysis of ENM rendered an observed I value of 0.421 that was among, or even was slightly higher than, the

null values (Fig. 5). This result suggests that climatic niches of both clades are similar, but not identical, according to the climatic background. For instance, the ENMs predictions were asymmetric for the two clades. The eastern Mexico + Central and South America clade predicted some areas along western Mexico coast as suitable, whereas the ENM for the western Mexico clade over-predicted as suitable some areas in northern Central America and a isolated area in western Ecuador. This is remarkable given that the latter is the range of *P. l. baroni*, which is sister to Central American-eastern Mexican *P. longirostris* (Fig. 1). Both geographic projections of ENMs (Figs. 5B and 5C) showed that environmental conditions in central and southern Oaxaca are not suitable for any clade.

Discussion

Phylogenetic analyses depict clearly the difference between western and eastern Mexican populations of *P. longirostris*, and indicated that *P. l. baroni* from Ecuador, a taxon considered by some as a full species (Hartert 1897; Hinkelmann 1996), is sister to the eastern Mexico + Central America clade, whereas the clade comprising western Mexican populations is sister to the eastern Mexico + Central America + Ecuador clade. The fact that one nDNA marker (locus 20454) showed differentiation among western and eastern Mexican populations is further evidence of the evolutionary independence of the clades. Nuclear DNA exhibits higher effective population size and lower mutation rates than mtDNA (Hare 2001; Zhang & Hewitt 2003), making it difficult to find fixed differences among populations of a single species. The GAPDH allele shared between western and eastern Mexican populations, was the most common allele and may indicate incomplete lineage sorting. Our morphometric analysis paralleled the results of Hinkelmann (1996), showing a clear separation between both eastern and western Mexican populations. Individuals from western Mexico were generally larger, and easily diagnosable by tail length.

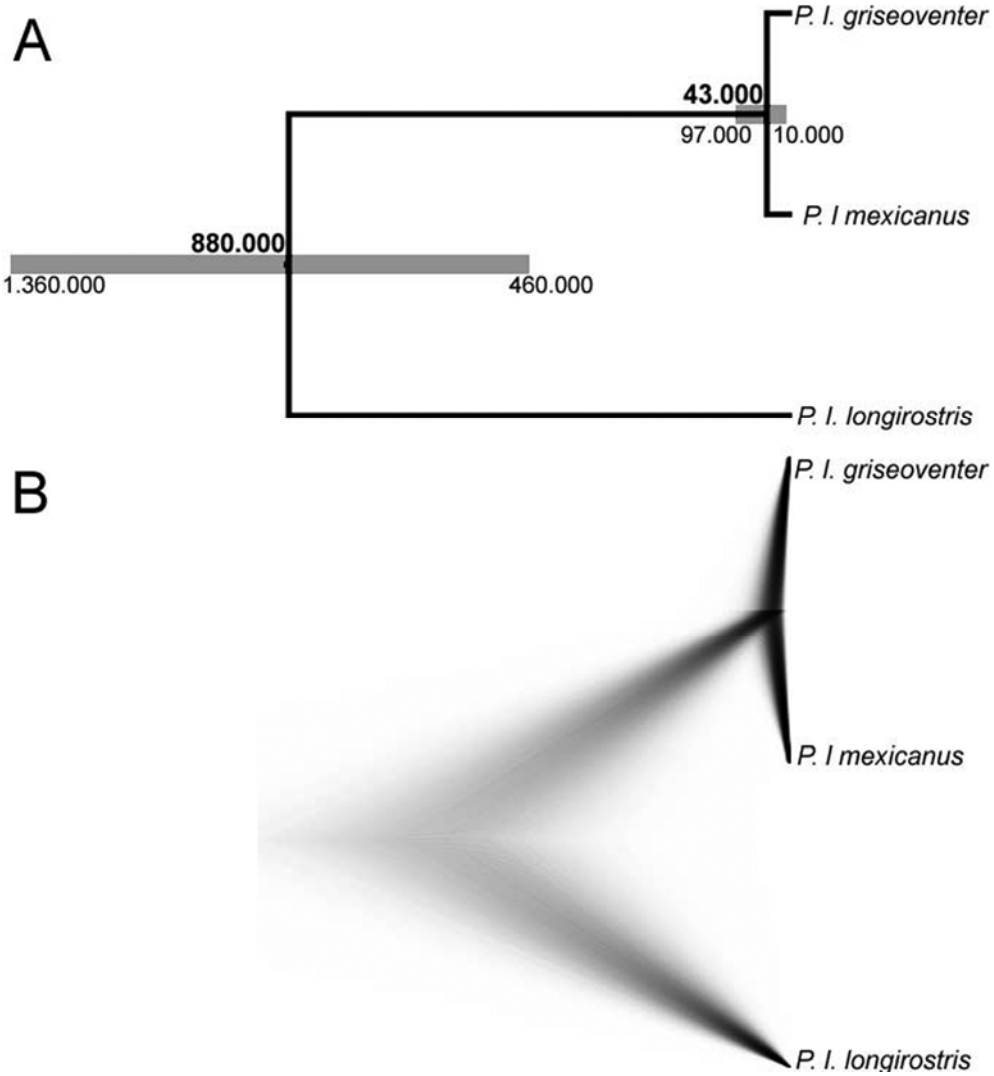

FIGURE 3. Species tree. A) Time divergence estimates in years (HPD and 95% confidence interval). B) Densitree showing all trees of the *BEAST analysis. Intensity depicts the congruence among different topologies and branch lengths.

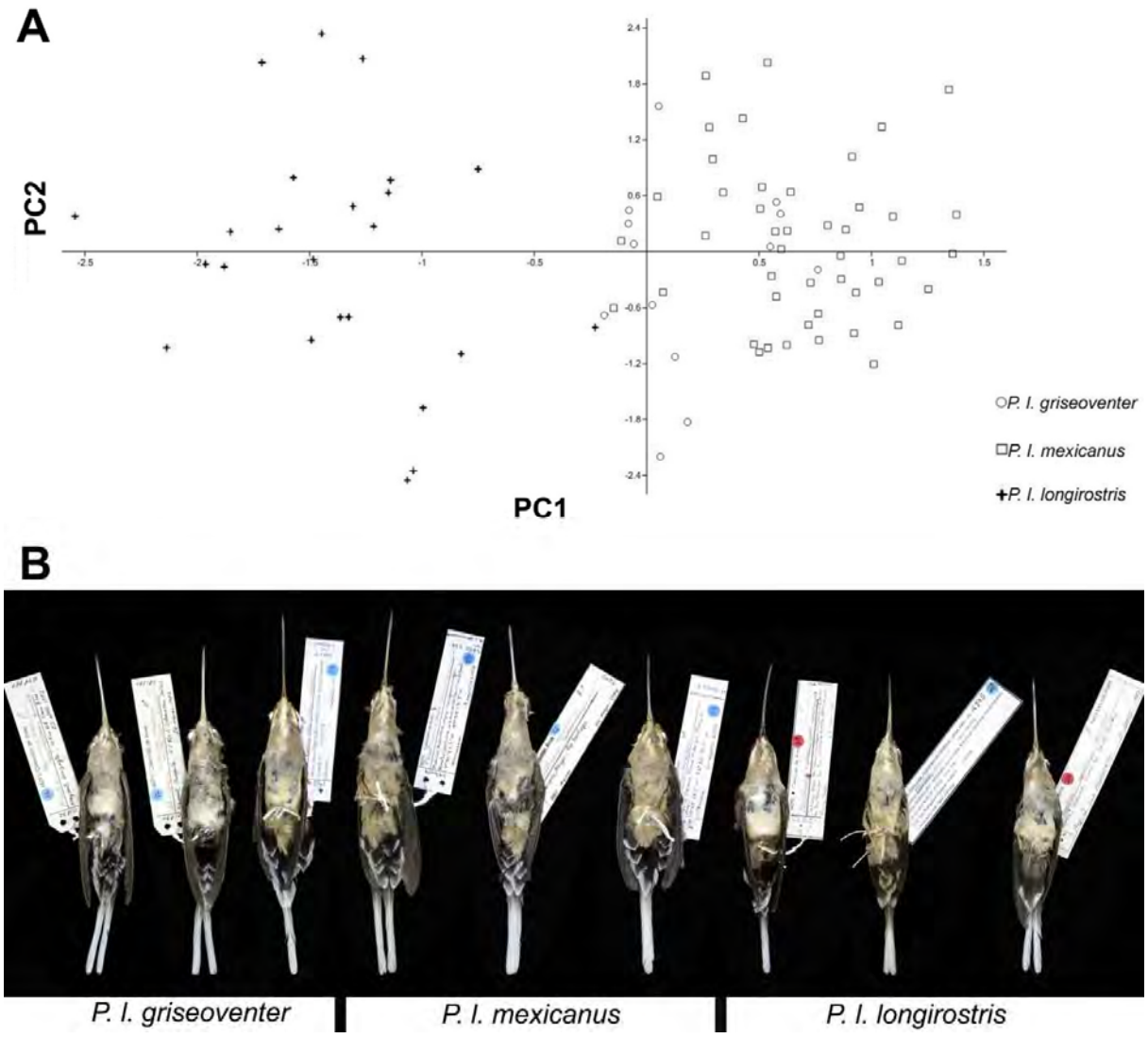

FIGURE 4. Morphological traits. A) Scatter plot of a PCA including morphometric measurements of the Mexican taxa of *P. longirostris* 'sensu lato'. B) Series of specimens representing the three Mexican subspecies of *P. longirostris* 'sensu lato'. Individuals from western Mexico (*P. l. griseoventer* and *P. l. mexicanus*) are characterized by larger tails with white tips to the outer rectrices, whereas those from eastern Mexico (*P. l. longirostris*) have shorter tails and some degree of rusty buff (varying from slight to heavy), excepting the last individual for which those tail feathers are lost. Note that an individual from Jalisco (third from left to right) shows a plumage similar to *P. l. mexicanus* but mtDNA haplotypes of *P. l. griseoventer.*

Using the criteria of Helbig et al. (2002) and Padial et al. (2010) (i.e., that species are groups fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, and whose differences correspond to or exceed the level of divergence seen in related sympatric species) to determine the taxonomic status of western Mexican *Phaethornis*, we found that the molecular evidence, when added to previous and new morphological information and to the recent description of the voices of both taxa (Howell 2013), supports separation of western Mexico populations as *Phaethornis mexicanus* Hartert 1897, as applied by Howell & Webb (1995) and Gill & Wright (2006). *Phaethornis mexicanus* is sister to *P. longirostris*, and represents the northernmost species in the hermit group. Morphological evidence has long been used to recognize the western Mexico populations of *P. longirostris* as distinct (Hartert 1897; Phillips 1961; Howell & Webb 1995; Hinkelmann 1996). These populations were described as the species *P. mexicanus* based on a specimen series from the states of Guerrero (type locality in Chilpancingo) and Jalisco because they "differ very conspicuously in having the outer rectrices tipped with white, instead of rusty buff" because "the tail is 3 to 5 mm longer" and because "the middle line of the throat [is] lighter and therefore more conspicuous" (Hartert 1897). Our analyses of both tail characters in

a series of *P. mexicanus* from the states of Nayarit, Jalisco, Guerrero, and Oaxaca, indicate that they are effective in separating these populations from the eastern Mexican *P. longirostris*. Our results parallel those of Hinkelmann (1996), who found that *P. mexicanus* (*P. l. mexicanus* and *P. l. griseoventer*) have larger mean measures for bill, wing, and tail length than *P. longirostris*. Despite those differences, Hinkelmann (1996) reports three specimens of intermediate coloration and overlap in linear measurements. Our series of individuals included one specimen with 'intermediate' measures, but it was not from a geographically intermediate locality. Moreover, the closer approach between *P. mexicanus* and *P. longirostris* (according to museum vouchers) is 155 km, indicating that an area of sympatry is unlikely (see also Howell 2013).

Phillips (1961) described the northernmost populations, from Nayarit and Jalisco, as *P. l. griseoventer*, based on subtle differences in color and color intensity. Some authors have considered *P. l. griseoventer* a full species under the phylogenetic or evolutionary species concept (Hinkelmann 1996; Navarro-Sigüenza & Peterson 2004). We found shallow mtDNA phylogeographic structure between northern and southern populations of *P. mexicanus*, but the alleles of the nuclear loci were shared by individuals throughout the range of *P. mexicanus*. In addition, these populations did not exhibit morphometric differences in the traits measured, and variation in color intensity did not clearly divide populations, as can be observed in the specimen from Jalisco in Figure 4B. Therefore, we consider that *P. l. griseoventer* represents recent intraspecific differentiation in *P. mexicanus*.

A proper definition of niche conservatism is not easy because this concept comprises a continuum, ranging from niches that are identical to niches that are more similar than random (Warren et al. 2008). The asymmetric predictions of the ENMs of both clades (particularly that *P. mexicanus* localities rendered a low prediction of the range of *P. longirostris*) as well as the results of an exploratory PCA of climatic variables from specimen localities (data not presented) indicated some degree of climatic specialization in *P. mexicanus* versus *P. longirostris*. The I value of 0.421 is among, or even below, the values found in other sister species of Mexican and North American animals (Warren et al. 2008; Pyron & Burbrink 2009). However, the background test did not support a scenario of niche differentiation, paralleling the results of previous studies comparing other sister species (Warren et al. 2008; McCormack et al. 2009). Thus, our results may indicate that the environments of *P. longirostris* in eastern Mexico, Central, and South America include some areas with climatic conditions similar to those of western Mexico. For instance, the geographical projections of the ENM of *P. mexicanus*, predicts the area of western Ecuador where the subspecies *P. l. baroni* ranges. Therefore, in the absence of strong evidence of climatic niche differentiation among clades and because the patterns of their ENMs indicated a climatically unsuitable area across southern Oaxaca, we consider that an alternative process, such as vicariance, could be involved in their differentiation (Peterson et al. 1999; Graham et al. 2004; Kozak & Wiens 2006).

We acknowledge that a potential error exists around the mean rates of evolution used here, even though they are mainly based on calibrations using geological or fossil information (Weir & Schluter 2008; Lerner et al. 2011). However, in the absence of other more accurate methods of dating we consider that our approach is useful for estimating a general timeframe for the speciation of *P. mexicanus* in western Mexico. The hermits are mostly limited to lowland forests; and only a few species occur above 2000 m (Navarro 1992; Stiles 2004), apparently because they don't have morphological plasticity for high altitude adaptation (Stiles 2004). Therefore, the highlands of central Oaxaca and Sierra Madre del Sur could be related with this speciation process. Our data suggest that evolutionary differentiation between *P. mexicanus* and *P. longirostris* occurred during the last 880,000 years, a time frame that is very recent to consider the orogenesis of the Sierra Madre del Sur (35–20 million years ago, Morán-Zenteno et al. 2000) as the factor promoting the differentiation. However, climatic oscillations during the Pleistocene (Webb & Bartlein 1992; Metcalfe et al. 2000; Caballero et al. 2010; Ceballos et al. 2010; Ferrusquía-Villafranca et al. 2010), likely made possible a connection between the lowland forest of eastern Mexico and the western Mexican tropical dry forest along the southern coast of Oaxaca, which at present is a region where both tropical dry forest and savanna coexist (Pérez-García & Meave 2006), and encompasses environmental conditions unsuitable for both species (Figs. 5B and 5C). In fact, it has been already considered that the speciation processes among the species group *P. longirostris*/*P. superciliosus*/*P. malaris* was facilitated by paleoclimatic-vegetational events and reinforced by geographical barriers (Hinkelmann 1996). Our analysis also highlighted genetic differentiation of *P. l. baroni*, which also inhabits 'drier' forest habitats in western Ecuador, from the rest of *P. longirostris*. This parallel event is suggestive of two instances of peripatric speciation in opposite points of the geographic distribution of *P. longirostris* "sensu lato" associated with the existence of drier ecosystems.

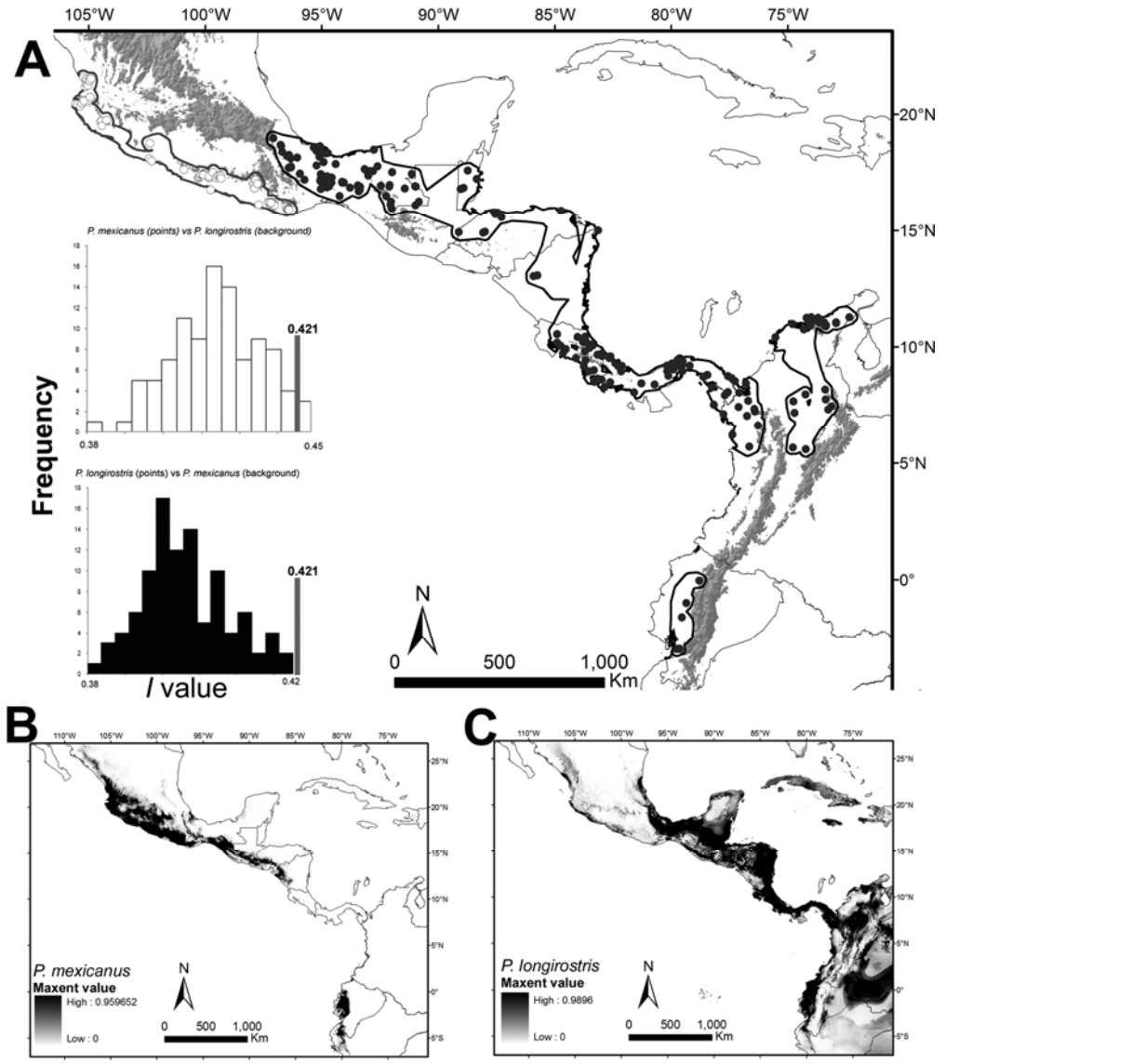

FIGURE 5. Climatic niche model results. (A) Map depicting the locality of each voucher used in the ENM for each clade (*P. mexicanus* in white and *P. longirostris* in black). The enclosed area around the points corresponds to the background used in the niche comparison of each species. Inset graphs depict the frequency histograms of the I null values for each test comparing the niches between clades. The calculated value among species is indicated with a gray line. (B-C) Maxent environmental niche model projected into the geography for each species/clade.

The results of this work agree with conclusions of other studies indicating that Mesoamerica has been a place for speciation of various bird lineages, including hummingbirds (e.g., García-Moreno et al. 2004; García-Moreno et al. 2006; García-Deras et al. 2008; Navarro-Sigüenza et al. 2008; González et al. 2011; Arbeláez-Cortés et al. 2012). In addition, this work contributes to a growing body of evidence indicating an active diversification of endemic lineages in the northern Neotropical dry forest region (e.g., Devitt 2006; Becerra & Venable 2008; Zarza et al. 2008; De-Nova et al. 2012), and reinforces the idea that western Mexico is a hotspot of endemism (45 endemic bird species, Peterson & Navarro 2000), and thus an important area for the study of the recent lineage diversification in Neotropical biotas.

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Appendix. List of individuals sequenced for this study, indicating collecting localities and GenBank accession numbers for DNA sequences.

Taxon	Collection number	State	Locality	Longitude	Latitude	ND2	COI	20454	GAPDH
Phaethornis longirostris	YACH 014	CHIAPAS	Porción norte de la Omega, Monumento Natural Yaxchilán	-90.973	16.902	KF525853	KF525875	KF525892	KF525915
Phaethornis longirostris	YACH 222	CHIAPAS	Curva noreste de la Omega, Monumento Natural Yaxchilán	-90.973	16.902	KF525854	KF525876	KF525893	KF525916
Phaethornis longirostris	YACH 306	CHIAPAS	Curva noreste de la Omega, Monumento Natural Yaxchilán	-90.973	16.902	KF525855	KF525877	KF525894	KF525917
Phaethornis longirostris	YACH 382	CHIAPAS	Campamento Arqueológico INAH de Yaxchilán	-90.983	16.906	KF525856	KF525878	KF525895	KF525918
Phaethornis longirostris	CHIMA 429	OAXACA	La Cabaña, 6.2 km NO de San Francisco La Paz	-94.050	17.067	KF525867	KF525879	KF525896	
Phaethornis longirostris	CHIMA 394	OAXACA	Chalchijapa, a 20 km NE del pueblo	-94.583	17.067	KF525868	KF525880		KF525919
Phaethornis mexicanus	PLU 248	OAXACA	Pluma Hidalgo	-96.423	15.927	KF525857	KF525881	KF525897	KF525920
Phaethornis mexicanus	PLU 290	OAXACA	Pluma Hidalgo	-96.423	15.927	KF525858	KF525882	KF525898	KF525921
Phaethornis mexicanus	PLU 315	OAXACA	Pluma Hidalgo	-96.423	15.927	KF525859	KF525883	KF525899	KF525922
Phaethornis mexicanus	PLU 276	OAXACA	Pluma Hidalgo	-96.423	15.927	KF525869	KF525884	KF525900	KF525923
Phaethornis mexicanus	CONACYT04 180	OAXACA	Finca El Brasil	-96.557	16.079	KF525860	KF525885	KF525901	KF525924
Phaethornis mexicanus	CONACYT04 221	OAXACA	Finca El Brasil	-96.557	16.079	KF525861		KF525902	KF525925
Phaethornis mexicanus	BMM 274	OAXACA	Sierra Miahuatlán, Río Salado 10 km N San Gabriel Mixtepec	-97.183	16.100				KF525926

Phaethornis mexicanus	OMVP 0717	OAXACA	Putla, cerca de Santa Ana del Progreso	-97.888	16.820	KF525870	KF525886	KF525903	KF525927
Phaethornis mexicanus	OMVP 0172	OAXACA	Putla, El Amate	-97.907	16.963	KF525871	KF525887	KF525904	KF525928
Phaethornis mexicanus	SRSC 091	GUERRERO	Monte Gallina 6 km W de San Cristobal	-100.065	17.396	KF525862	KF525888	KF525905	KF525929
Phaethornis mexicanus	SRSC 076	GUERRERO	Monte Gallina 6 km W de San Cristobal	-100.065	17.396			KF525906	KF525930
Phaethornis mexicanus	SIT 68	GUERRERO	Nueva Delhi, San Francisco	-100.195	17.422	KF525872	KF525889	KF525907	KF525931
Phaethornis mexicanus	CAON 141	GUERRERO	El Varillal	-100.913	17.625	KF525863		KF525908	KF525932
Phaethornis mexicanus	CAON 142	GUERRERO	El Varillal	-100.913	17.625	KF525864		KF525909	KF525933
Phaethornis mexicanus	FRG 209	NAYARIT	Pintadeño, 11 km SW tepic	-104.960	21.418	KF525865		KF525910	KF525934
Phaethornis mexicanus	KABS 737	NAYARIT	El Cuarenteño, Sierra San Juan	-105.087	21.492				KF525935
Phaethornis mexicanus	FRG 381	NAYARIT	Palapita, 18.5 km S Jalcocotán	-105.095	21.303			KF525911	KF525936
Phaethornis mexicanus	FRG 187	NAYARIT	Palapita, 21 km S Jalcocotán	-105.095	21.297	KF525866		KF525912	KF525937
Phaethornis mexicanus	URRA57	JALISCO	Los jardines botanicos de Vallarta, Mpio. Cabocorrientes	-105.294	20.466	KF525873	KF525890	KF525913	KF525938
Phaethornis mexicanus	URRA30	JALISCO	Rancho Primavera, El Tuito, Mpio. Cabo Corrientes	-105.358	20.345	KF525874	KF525891	KF525914	KF525939

CAPÍTULO 2

Multilocus phylogeography and morphology give insights into the recent evolution of a Mexican endemic songbird: *Vireo hypochryseus* ☼

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Multilocus phylogeography and morphology give insights into the recent evolution of a Mexican endemic songbird: *Vireo hypochryseus*

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Abstract.

We used multilocus phylogeographic analyses, morphometric measurements, and environmental niche models (ENMs) to analyze the recent evolution of the Golden Vireo (*Vireo hypochryseus*), a Mexican endemic species. *Vireo hypochryseus* is made up of two phylogeographically structured mitochondrial DNA clades that probably diverged 132,000 years ago. One clade comprised individuals from mainland Sinaloa and the Tres Marías islands in the northwest, and the other included individuals from the remaining range of the species. This marked phylogeographic structure contrasts with the low genetic structure reported for temperate North American vireos. The nuclear DNA markers also showed some geographic differences in allele frequency, but did not exhibit a clear phylogeographic structure. The morphometric analyses suggested a decreasing north to south cline, with the largest individuals located in the Tres Marías islands. The ENMs did not support a scenario of geographic fragmentation of the environmental conditions of the area in which *V. hypochryseus* has inhabited over the last 130,000 years. However, a model of isolation by resistance based on the actual configuration of climatic conditions in western Mexico did explain a major proportion of both the mitochondrial DNA distances and the differences in size, while a model of isolation by distance explain a low proportion of such differences. Therefore, the recent history of *V. hypochryseus* was likely shaped by historical habitat fragmentation due to fluctuating environmental conditions in the mainland that produced a phylogeographic print, and natural selection on morphological traits in the insular population, suggesting an active diversification of endemic lineages in the Mexican dry forest.

Neotropical bird species exhibit marked patterns of genetic structure matching the presence of biogeographical barriers, and are often accompanied by morphological differentiation (e.g., Navarro-Sigüenza et al. 2008, Kerr et al. 2009, Peterson and Navarro-Sigüenza 2009, Weir 2009, Barber and Klicka 2010, Tavares et al. 2011, Milá et al. 2012, Naka et al. 2012). In contrast, birds in temperate North America exhibit low intraspecific genetic differentiation that is usually explained by a rapid range expansion driven by paleo-climatic changes (Zink 1996, Hebert et al. 2004, Kerr et al. 2007, Milá et al. 2007, Zink et al. 2010, Klicka et al. 2011, Smith et al. 2011). These contrasting patterns have been also found in studies of congeneric bird species that show low genetic structure in the temperate zone and a marked geographic structure in Mexico and Central America (e.g., Milá et al. 2007, McCormack et al. 2011, Klicka et al. 2011, Smith et al. 2011, Bryson et al. In press). Therefore, differences in the level of phylogeographic structure seem to reflect distinct climatic histories in both regions.

The genus *Vireo* is a taxon widespread across the Americas. It includes 31 species, of which about 18 are range-restricted, including some endemic to the Caribbean islands (Gill and Donsker 2013). Most *Vireo* species are divided into several subspecies (between 2 and 13; Gill and Donsker 2013), which is suggestive of differentiation due to isolation on islands, and the occurrence of intraspecific genetic structure among populations. However, some studies have shown that temperate *Vireo* species do not exhibit genetic structure (Cicero and Johnson 1998, Zwartjes 1999, Zwartjes 2001, Hebert et al. 2004, Barr et al. 2008, Zink et al. 2010), whereas the South American *V. olivaceus* exhibited recognizable parapatric lineages (Kerr et al. 2009,

Tavares et al. 2011). Moreover, Caribbean endemic species and populations exhibit low genetic diversity (Zwartjes 1999, Zwartjes 2003, Tavares et al. 2011), with only a shallow correspondence between morphometric and genetic variation (Zwartjes 2003). Therefore, variation on such traits probably could be due to different factors.

The Golden Vireo (*Vireo hypochryseus*) is endemic to Mexico, and includes mainland and island populations (Howell and Webb 1995, Gill and Donsker 2013). Although this species is relative wide range in Mexico the majority of its range is in western Mexico. The predominant vegetation type in this region is the tropical dry forest (or seasonally dry tropical forests) an endangered ecosystem where several biogeographic breaks had been discovered in several taxa (see Arbeláez-Cortés et al. 2014). Three subspecies are recognized: *V. h. hypochryseus* (Sclater 1862) from mainland western Mexico (Sinaloa to Oaxaca), *V. h. sordidus* (Nelson 1898) from the Tres Marías islands (a Mexican archipelago in the Pacific Ocean located about 100 km offshore Nayarit), and *V. h. nitidus* (van Rossem 1934) from northwestern Mexico (southern Sonora). The form of the Tres Marías islands was described by Nelson (1898) on the basis of differences in plumage and bill color and in bill size. This population also has higher average size measurements in comparison to mainland populations (Nelson 1898, Grant 1965). Therefore, the phylogeographic analysis of *V. hypochryseus* can be used to test two alternative hypotheses regarding the Tres Marías islands taxon. (1) If this insular taxon diverged long ago in the region we would expect to find genetic differences across different loci. Alternatively, (2) if the insular population does not show clear differences in molecular markers compared with the mainland populations, the

evolution of their phenotypic traits could be considered as an output of recent natural selection.

We used a multilocus molecular dataset to test whether *V. hypochryseus* exhibits phylogeographic structure and to set a time frame for its intraspecific differentiation. We also searched for congruence between genetic distances, morphometric differences, and geographical and ecological (i.e., resistance) distances. In addition, we examined whether there is congruence between genetic variation and climatically stable areas over the last 130,000 years, as defined using environmental niche models (ENMs).

Material and Methods

Sampling and laboratory procedures

Tissue samples were obtained from specimens deposited in the ornithological collection of the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC, Appendix). The samples include both the wide range mainland subspecies *V. h. hypochryseus* and the insular *V. h. sordidus*, but not include *V. h. nitidus* described from southern Sonora from a single individual and probably representing the populations ranging in the northernmost area (van Rossem 1934, Gill and Donsker 2013). Genomic DNA was isolated from frozen or ethanol-preserved tissues by a NaCl and chloroform:isoamyl alcohol mix method or using the Qiagen DNEASY^{TM} kit (Qiagen Inc., Valencia, CA, USA). Both maternally inherited mtDNA and bi-parentally inherited nDNA sequences were obtained. The mtDNA subunit 2 nicotinamide adenine dinucleotide dehydrogenase gene (ND2) was amplified using primers H6313 and L5216 or L5219 (Sorenson et al. 1999), specific internal primers

designed de novo for this study (eac-ND2LInt1: 5'CTTAACCAAACKCAAATCC 3' and eacND2Hin3: 5' GGGTTAGCTTAGGGTTGTAGA 3'), or the primers H1056U and L5215U (H. Vázquez-Miranda pers. comm.). We also amplified and sequenced the following four nuclear DNA regions: (1) locus 20454 using primers 20454F and 20454R (Backström et al. 2008); (2) intron 11 of glyceraldehyde-3-phosphate dehydrogenase (GAPDH) using primers GapdL890 and GapdH950 (Friesen et al. 1997); (3) muscle-specific kinase receptor intron 3 (MUSK) using primers MUSK-I3F and MUSK-I3R (Kimball et al. 2009); and (4) transforming growth factor beta 2 intron 5 (TGFB) using primers TGFB2.5F and TGFB2.6R (Sorenson et al. 2004). All DNA regions were amplified by PCR in 15 µl reactions including 1x PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM each dNTP, 0.4 – 0.5 µM each primer, 1 - 2 unit DNA polymerase, and around 50 - 100 ng of DNA. All PCR procedures included negative controls to check for contamination. PCR protocols are in Table S1 (see supplemental material). PCR products were visualized in agarose gels stained with ethidium-bromide and purified using Exo-SAP-IT™ (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA). The sequences were obtained by ABI Prism BigDye™, version 3.1 (Qiagen Inc., Valencia, CA, USA) terminator chemistry, using the same primers as for each PCR in an ABI 3730XL automated sequencer. They were edited and aligned manually using BioEdit, version 7.0.5 (Hall 1999). For the nDNA sequences we inspected all chromatograms to detect double peaks, which were edited by coding them as standard IUPAC ambiguities. Each polymorphic nucleotide position was then scanned across all individuals to check for accuracy and consistency in the identification of double peaks. The allele phase of each nDNA locus was resolved using the coalescent-based Bayesian method of the Phase

algorithm (Stephens et al. 2001, Stephens and Donnelly 2003) in DnaSP, version 5 (Librado and Rozas 2009) using 10,000 iterations, 10 thinning intervals, 1,000 iterations as burn-in, allowing for recombination, and setting an output probability threshold of 0.9. We used the resulting highest-probability haplotypes for further analyses. All sequences have been deposited in GenBank (##### - #####, Appendix).

Phylogenetic and phylogeographic analyses

The software BEAST, version 1.7.4 (Drummond et al. 2012a, Drummond et al. 2012b) was used to reconstruct phylogenetic relationships among haplotypes. First, we analyzed 1020 bp of ND2 of 15 unique haplotypes from 34 *V. hypochryseus* plus sequences from the GenBank for other 5 *Vireo* species, using the more distantly related vireonid *Cyclarhis gujanensis* as an outgroup. Second, we used *BEAST (Heled and Drummond 2010) in BEAST 1.7.4 to calculate divergence time between the two major clades identified in the ND2 analysis, using the multilocus dataset (i.e., ND2, 20454, GAPDH, MUSK, and TGFB). *BEAST uses the multispecies coalescent model and allows including information from independent loci in a single, non-concatenated, analysis to obtain a species tree estimating the time when ancestral species diverged in two (Heled and Drummond 2010). The best-fit model for each locus was selected using Akaike's information criterion in Modeltest, version 3.7 (Posada and Crandall 1998). We ran BEAST and *BEAST for 200 million generations, sampling every 2,000 steps, using a Yule speciation tree prior, a UPGMA starting tree, a log normal relaxed uncorrelated molecular clock, and mutation rates of 2.9×10^{-8} substitutions/site/year for the ND2 , 1.67×10^{-9} substitutions/site/year for the 20454, 1.2×10^{-9} substitutions/site/year for

the GAPDH, and 1.7 x10 $^{-9}$ substitutions/site/year for TGFB and MUSK, according to rates reported previously for those or similar genes in birds (Lim and Sheldon 2011, Manthey et al. 2011, Sly et al. 2011, Smith and Klicka 2010, Weir and Schluter 2008, Lerner et al. 2011). Because MUSK is a Z-linked gene (Kimball et al. 2009) their hemizygosis was considered in the analysis by setting the ploidy type as X while constructing the BEAUTY (Drummond et al. 2012b) file. After the analysis, we used TreeAnnotator, version 1.7.4 (Rambaut and Drummond 2012), to generate a tree-file compiling the data, using a 25% burn-in and a posterior probability limit of 0.5. We also constructed networks for each locus using the median-joining algorithm in Network version 4.6 (Bandelt et al. 1999) and mapped the allele/haplotype frequency using ArcGis, version 9.3 (ESRI 2009). Afterwards, we used DnaSP to calculate values of genetic diversity for the whole range of the species, and for both the Tres Marías islands and the continental samples.

Morphometric traits

We measured standard morphological traits of all specimens of *V. hypochryseus* housed in MZFC at UNAM (63 individuals, from 26 localities), with a Mitutoyo Absolute Digimatic caliper (to the nearest 0.01mm). Measurements included: total culmen length, exposed culmen length, nostril to tip length, bill depth, bill width (measured at the center of the nostrils), tarsus length, tail length, and wing chord. To check for variation in these measurements, all individuals were measured two times and those values were compared using correlation coefficients in PAST (Hammer et al., 2001). After corroborating that variation among measurements was null or low, all individuals were

measured a third time and only these last measurements were used in the analyses. We included only adult individuals of known sex (according to skull ossification and gonadal information). Afterwards, we determined which measurements varied among sexes by comparing mean and variance with a Mann-Whitney test. The measurements that did not differ among sexes were correlated with each other and those exhibiting high correlation ($r > 0.6$) were excluded. We used the remaining measurements for further analysis, by considering only the individuals for which all measurements were available. We conducted a Principal Component Analysis (PCA) in PAST to investigate whether morphometric variation is geographically structured, and to define an index of overall size variation among individuals to be used in comparisons with other data sets. We then used Mann-Whitney tests to compare each measurement between individuals from the Tres Marías islands and the continent.

Definition of climatic stable areas through ENMs

We constructed ENMs with data for the present and projected them onto one present and two past environmental scenarios to define climatically stable areas. We included 19 bioclimatic variables from WorldClim (Hijmans et al. 2005) and three topographic layers from the Earth Resources Observation and Science Center (EROS 2011). The palaeo-environmental layers were drawn from the general circulation model simulations from the Community Climate System Model and the Model for Interdisciplinary Research on Climate for the Last Glacial Maximum (21,000 years ago) and the Last Interglacial Period (130,000 years ago). The bioclimatic layers were the ones available at WorldClim Global Climate Data Version 1.4 (WorldClim 2012). A total of 179 unique

localities of collection of *V. hypochryseus* were gathered from the atlas of the birds of Mexico database (Navarro et al. 2003). All layers were clipped with a polygon around the most external localities plus a 50 km buffer. To use only uncorrelated layers, the environmental data of every locality was extracted and subjected to a correlation test among layers using PAST, and excluded one of every pair of layers with $r > 0.9$. We run 10 replicates in Maxent version 3.3 (Phillips et al. 2006), using cross-validation and without clamping in the projections. Afterwards, we chose the model with the highest Receiver Operating Characteristic Area Under the Curve for the test data. Once the best model was selected, we defined presence-absence values by selecting the logistic threshold of the test omission rate closer to 10%. Such threshold was then applied to the projections in the palaeoclimatic and present layers. We defined climatic stable areas (e.g., Carnaval et al. 2009) over the last 130,000 years by multiplying the predicted presence/absence maps (i.e., pixel values of 1 and 0) using the raster calculator of ArcGis.

Congruence among distance matrices

We used an analysis of Congruence Among Distance Matrices (CADM, Legendre and Lapointe 2004) in R (R Development Core Team, 2012) by using APE 2.5-2 (Paradis et al. 2004) to assess the congruence between geographic, environmental and genetic distances (comparing genetic distances on both the ND2 and the GAPDH) as well as with morphometric variation among individuals. CADM tests the hypothesis that several matrices containing different types of variables about the same objects (in this case genetic distances for mtDNA and nDNA, size differences, and geographic and

ecological distances among individuals) are congruent. This analysis was limited to 22 individuals from nine localities, for which we obtained both ND2 and GAPDH sequences as well as the complete set of size measurements. The rest of the nDNA markers were not used for this analysis since they were available only for a few individuals. The K2P distances among individual pairs were thus calculated in MEGA version 5.2 (Tamura et al. 2011). Given that there are two copy for each nDNA locus per individual, we used the mean K2P distances among the alleles of each individual pair as the distance to compare. We used the first principal component values (which explained the majority of the variance and was correlated positively with all measurements, see below) as an index of overall size variation among individuals. Geographic distance was included as the linear distance in kilometers among individuals, while the 'environmental' distance (i.e., resistance distance) was calculated using the method proposed by McRae (2006), which estimates values of resistance among localities considering a user defined resistance layer. In this case, the resistance layer was the inverse of the best ENM obtained in Maxent using the raster calculator in ArcGis (i. e., 1-Maxentmodel). The original Maxent layer presented values for each pixel that could be interpreted as the probability of occurrence of the optimal conditions where the species inhabits; therefore the inverse layer represents higher values (i.e., high resistance) for those zones where the species does not occur. Geographic and resistance distances are conceptually different, because the former assumes spatial homogeneity and only one way to connect pairs of localities, whereas the latter takes into account landscape heterogeneity and multiple ways to connect pairs of localities. All distance matrices were standardized between 0 and 1 before performing the CADM. A global CADM test

was carried out to assess overall congruence among matrices, and was followed by an *a posteriori* pair-wise CADM and one-tailed Mantel tests to identify which combinations of matrices were congruent. We used 999 permutations to assess significance and the Holm correction for multiple comparisons.

Results

All loci were polymorphic, but the number of alleles and nucleotide diversity varied among them (Table 1). The nucleotide diversity of the mtDNA was twice the diversity found for GAPDH, which was the most polymorphic of the nuclear loci. Almost all alleles and haplotypes were found in mainland individuals. The exception was the ND2 haplotype exclusive from Tres Marías islands, which differed from the allele found in Sinaloa by just one mutation. This insular population showed null variation for almost all loci (Table 1), and always presented the most common and widespread alleles for all nDNA loci.

The ND2 (Fig. 1) showed that *V. hypochryseus* is composed of two well supported and geographically structured clades (*a posteriori* support = 0.99, Fig. 1). One clade comprised samples from Sinaloa and Tres Marías islands in the northwestern range of the species, while the other included the remaining samples (i.e., Jalisco, Guerrero, Oaxaca, and Hidalgo). The divergence time estimated in *BEAST between these clades was 132,000 years ago (HPD 95% from 246,000 to 53,000 years ago). The geographic range of the alleles from the nDNA also showed some degree of spatial structure. For example, common alleles of GAPDH and 20454 were restricted to

the southern and eastern samples (Fig. 2). As depicted in Figure 2 some alleles showed some kind of spatial structure between samples from Oaxaca (and some from Guerrero) and the remaining localities. However, as commented before, the Tres Marías islands individuals always presented the most common and widespread alleles of each nuclear marker.

From the eight morphological measurements obtained from 49 individuals, tail length and wind chord were statistically larger in males (Mann-Whitney test, all $P < 0.05$), and therefore were excluded from the remaining analyses to avoid differences related to sexual dimorphism. Nostril to tip length was highly correlated ($r > 0.6$) with other measurements and was also excluded. The Principal Components 1 and 2 explained most variation in size, 59% and 22.7% respectively. The PC 1 was highly and positively correlated with all measurements, especially tarsus length ($r = 0.86$), total culmen ($r = 0.77$), and nostril to tip length ($r = 0.73$). Therefore, this component divided the largest individuals from the rest. These largest individuals included 9 of the 10 individuals from the Tres Marías islands plus 2 individuals from Nayarit and 1 from Guerrero (Fig. 3). Four of the five measurements compared between the islands and the mainland were statistically larger in the insular specimens (Mann-Whitney test, all $P < 0.001$), excepting exposed culmen which showed no significant differences (Fig. 4).

The climatic stable areas were smaller than the current range of the species (Fig. 5), and were restricted to western Mexico. Despite the fact that the northwestern range of the species was not recovered as stable, and that the stable areas between Guerrero

and Oaxaca presented some fragmentation, this methodology suggested there was not a major division of the environmental conditions in the area in which *V. hypochryseus* has inhabited over the last 130,000 years.

The global CADM rejected the null hypothesis of incongruence among matrices (W = 0.6, *P* = 0.001), and the *a posteriori* CADM showed that almost every matrix pair was congruent. In general, the isolation by resistance model explained better the mtDNA distances and the differences in size than the simpler model of isolation by distance. The major congruence was found between the mtDNA genetic distances and both the resistance and geographic distances (Mantel correlation = 0.84 and 0.76, all *P* = 0.001). The mtDNA distance was also correlated, but with lower values, to the size differences among individuals and to the nDNA distances (Mantel correlation = 0.54 and 0.3, all $P < 0.01$). On the other hand, the nDNA distance was poorly, although significantly, correlated with both the geographic and resistance distances (Mantel correlation = 0.37 and 0.29, all $P < 0.01$), while the matrix for size differences among individuals was correlated with the resistance distances (Mantel correlation = 0.73, *P* = 0.001) but was incongruent with the nDNA genetic distances (Mantel correlation = 0.12, $P > 0.05$).

Discussion

This study shows that *V. hypochryseus* comprises two mtDNA lineages, which is congruent with the pattern found for other Neotropical birds that exhibit high levels of intraspecific variation (Navarro-Sigüenza et al. 2008, Burney and Brumfield 2009, Kerr et al. 2009, Peterson and Navarro-Sigüenza 2009, Vázquez-Miranda et al. 2009, Weir

2009, Arbeláez-Cortés et al. 2010, Barber and Klicka 2010, Tavares et al. 2011, González et al. 2011, Arbeláez-Cortés 2012, Milá et al. 2012, Naka et al. 2012, Ornelas et al. 2013), and contrasts with the low genetic structure reported for temperate *Vireo* species (Cicero and Johnson 1998, Zwartjes 1999, Zwartjes 2001, Hebert et al. 2004, Barr et al. 2008, Zink et al. 2010). The range of some nDNA loci's allele frequencies and particularly the congruence between GAPDH and ND2 genetic distances roughly support this major division of lineages. The lack of samples from Nayarit and most of Jalisco precludes locating with certainty the zone of phylogeographic break but it is clear that the break occurs in the mainland, along western Mexico, and not between the Tres Marías islands and the continent. In fact, the mainland region between Nayarit and Jalisco, where this break of *V. hypochryseus* ND2 is probably located, is also a putative contact zone for other birds such as *Calocitta colliei* - *C. formosa*, *Cyanocorax beechei* - *C. sanblasianus*, and *Ortalis wagleri* – *O. poliocephala* (e.g., Howell and Webb 1995). In this region, the highlands of the Transmexican Volcanic Belt are very close to the coast diminishing the breath of the lowlands where the Neotropical Dry ranges which is the main habitat for *V. hypochryseus*. It had been proposed that other mountain ranges in western Mexico are probably related with some kind of ecological/climatic instability (see Arbeláez-Cortés et al 2014) and this could be also the case for Transmexican Volcanic Belt. However, additional sampling around this zone is necessary to further explore this possibility. Our results also parallel those of other phylogeographic studies in the same region which have found similar phylogeographic breaks in a number of lowland species, ranging from snakes, birds, and freshwater fishes to ants and trees (Zaldívar-Riverón et al. 2004, Mateos 2005, Miller and Schaal 2005, Devitt 2006,

Mulcahy 2008, Zarza et al. 2008, Pringle et al. 2012, Arbeláez-Cortés and Navarro-Sigüenza 2013, Arbeláez-Cortés et al. 2014).

Our data also suggest that the differentiation between both mtDNA clades of *V. hypochryseus* occurred around 136,000 years ago, a time frame that is very recent to consider geological processes (Morán-Zenteno et al. 2000, Becerra 2005, Devitt 2006) as the main factors promoting genetic differentiation. An alternative explanation might be the climatic fluctuations during the Pleistocene in Mexico (Webb and Bartlein 1992, Metcalfe et al. 2000, Caballero et al. 2010) as an event promoting habitat fragmentation, reducing gene flow, and finally generating phylogeographic structure. However, despite that the time frame calculated for the major division agrees roughly with this scenario, the climatically stable areas obtained for the last 130,000 years did not show a marked division of the range of the environmental conditions in the area where *V. hypochryseus* inhabits. We did not rule out completely the alternative of climatic changes promoting phylogeographic structure given the fact that some discontinuities in the climatic stable areas were observed in Guerrero and Oaxaca. Such discontinuities could have diminished gene flow in the past, but probably were not the sole factor.

Other than past climatic fluctuations, present geographic or environmental barriers have also been considered to explain genetic structure in Neotropical birds (Weir 2009, Burney and Brumfield 2009, Arbeláez-Cortés 2012, Naka et al. 2012, Ornelas et al. 2013). We found a high correlation between the ND2 genetic distances and the resistance distances. In fact, we observed that some areas with relative high

resistance are placed around the Michoacán-Guerrero border. This region coincides with the division of sister species of snakes (*Porthidium* spp. and *Leptodeira* spp.; Bryson et al. 2008, Daza et al. 2009), and it is close to a zone of high diversification for the trees of the genus *Bursera* (Becerra 2005, Becerra and Venable 2008). However more samples of *V. hypochryseus* are necessary to examine further the role of this area in its intraspecific differentiation. We consider plausible that the phylogeographic pattern observed in *V. hypochryseus* is a result of a diminished gene flow due to recent past climatic changes combined with the present configuration of environmental conditions across its range.

We also found significant congruence among morphometric variation and both the mtDNA distances and the resistance distances. The first correlation is explained by the fact that larger individuals are found in the northern mainland and in the Tres Marías islands, which are areas where a different haplogroup is present. However, the differentiation in size was not discrete and we found overlap in measures among individuals from different haplogroups. The later correlation is probably explained by the high values of resistance assigned to the oceanic separation of Tres Marías islands from the continent and the larger sizes of individuals observed in this insular population. Several lines of evidence have indicated that birds follow the 'island rule', with large-bodied species getting smaller on islands and small-bodied species getting larger (Clegg and Owens 2002, Lomolino 2005, Boyer and Jetz 2010). In small birds, such as *V. hypochryseus*, the trend towards overall large-bodies in the islands is not simply due to changes in the feeding ecology, but it could be also associated to an intense

intraspecific competition and may be an adaptation for the high population densities observed on island populations (Clegg and Owens 2002, and references therein), which is the case for *V. hypochryseus* and other passerine populations in Tres Marías islands (see Grant 1965). Therefore, a role of natural selection in driving those differences is plausible because larger sizes are shared by the populations of different species in the same place.

Our molecular results also agree with the pattern found in *Icterus pustulatus* from Tres Marías islands which exhibits a single mtDNA haplotype differentiated only by one mutation from the most common haplotype in the mainland (Cortés-Rodríguez et al. 2008), but contrast with the strong genetic differentiation of *Cardinalis cardinalis mariae* (Smith et al. 2011, Smith and Klicka 2013). All three bird species from the Tres Marías islands mentionedhave populations that are phylogeographically more closely related to mainland populations in northwestern Mexico (i.e., Sonora, Sinaloa, and Nayarit). Geological and paleoecological evidence suggest that emerged land has been in the present position of the Tres Marías islands since mid-Pliocene, although it is thought that it was already insular in the Pleistocene, but separated from the mainland by as little as 13 km (Zweifel 1960, WorldClim 2012). Considering this information and the results obtained here, we suggest that Tres Marías islands population of *V. hypochryseus* derived from individuals from Nayarit-Sinaloa. In addition, the almost null genetic diversity observed in this insular population parallels the pattern found in other insular vireos (Zwartjes 1999, Zwartjes 2003, Tavares et al. 2011). Both natural selection and demographic processes might produce the same pattern of low genetic

diversity. However, selection affects the genome locally, whereas demography extends its effect on the whole genome, as observed here for the multilocus dataset. Although we considered natural selection to explain the larger measurements of island individuals, we consider that the low to null variation in different loci from the islands implies that effective historical population size has been low; suggesting that colonization of those islands was a consequence of a few individuals establishing a peripatric population there. In fact, another study using multilocus information also indicated a low historical population size for the Tres Marias *Cardinalis cardinalis mariae* (Smith and Klicka 2013).

The phylogeographic pattern of *V. hypochryseus* is similar to the one found for other taxa in the area, and contributes to a growing body of evidence indicating an active diversification of endemic lineages in the northwestern Mexican dry forest (Zaldívar-Riverón et al. 2004, Mateos 2005, Miller and Schaal 2005, Devitt 2006, Becerra and Venable 2008, Mulcahy 2008, Zarza et al. 2008, De-Nova et al. 2012, Pringle et al. 2012, Arbeláez-Cortés and Navarro-Sigüenza 2013, Arbeláez-Cortés et al. 2014). Altogether, these results raise this region as an important area to study the recent lineage diversification of Neotropical biotas. We conclude that the recent history of *V. hypochryseus* was not driven by a sole factor. Instead, their history includes phylogeographic differentiation in the mainland probably derived from stochastic processes after some reduction in geneflow between major areas, natural selection on morphometric traits, and a founder bottleneck in the Tres Marías islands.

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Tables

Table 1. Datasets (mtDNA and nDNA) obtained for *Vireo hypochryseus* from Mexico. Genetic diversity values (π =nucleotide diversity and H= haplotype number) are indicated for each marker both for the whole dataset and for the mainland and islands populations.

Locus	Total samples	Sequence length (bp)	Genetic diversity (π, H)		
			Vireo hypochryseus	Mainland	Tres Marias islands
ND2	34	1040	0.0087, 15	0.0047, 14	0, 1
GAPDH	31	328	0.0045, 6	0.0051, 6	0.0016, 2
20454	15	400	0.0023, 5	0.0027, 5	0, 1
MUSK	27	495	0.0006, 3	0.0009, 3	0, 1
TGFB	18	370	0.0013, 4	0.0018, 4	0, 1

Figures

Figure 1. Phylogeography of *Vireo hypochryseus* a Mexican endemic. Left, phylogenetic reconstruction of the mtDNA (ND2) data set. Right, the map depicts the range of each haplogroup (same color). Circles represent localities of the samples, and their sizes are proportional to sample size. Species range is shown in gray .

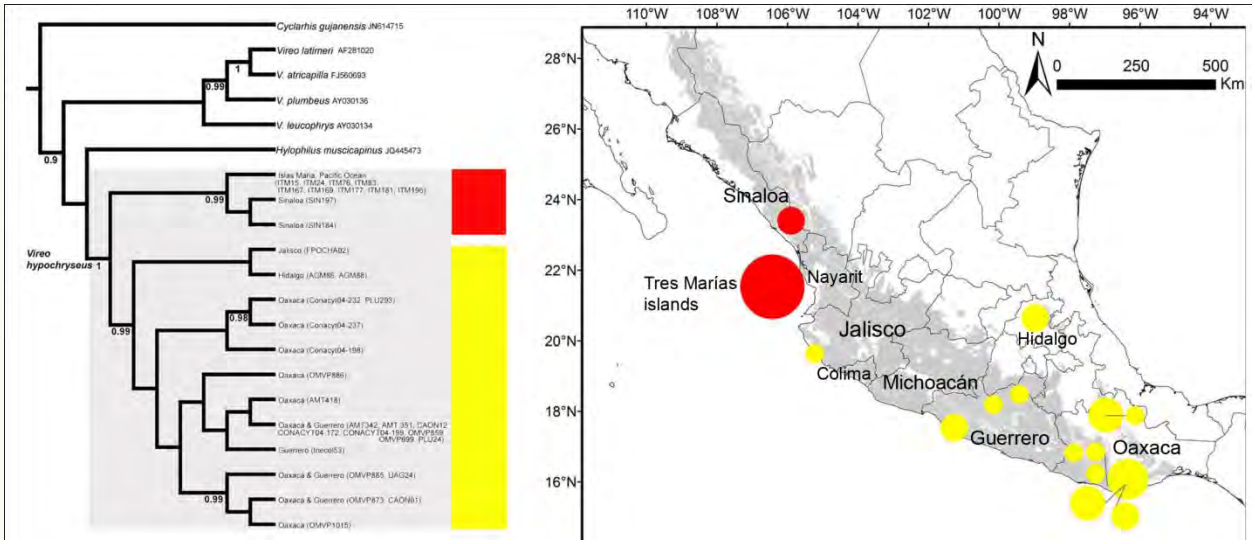


Figure 2. Allele networks of the nDNA for four loci of *Vireo hypochryseus*. Maps depict the range of each allele (same color). Circles in the maps, represent localities of the samples and their sizes are proportional to sample size. Species range is shown in gray.

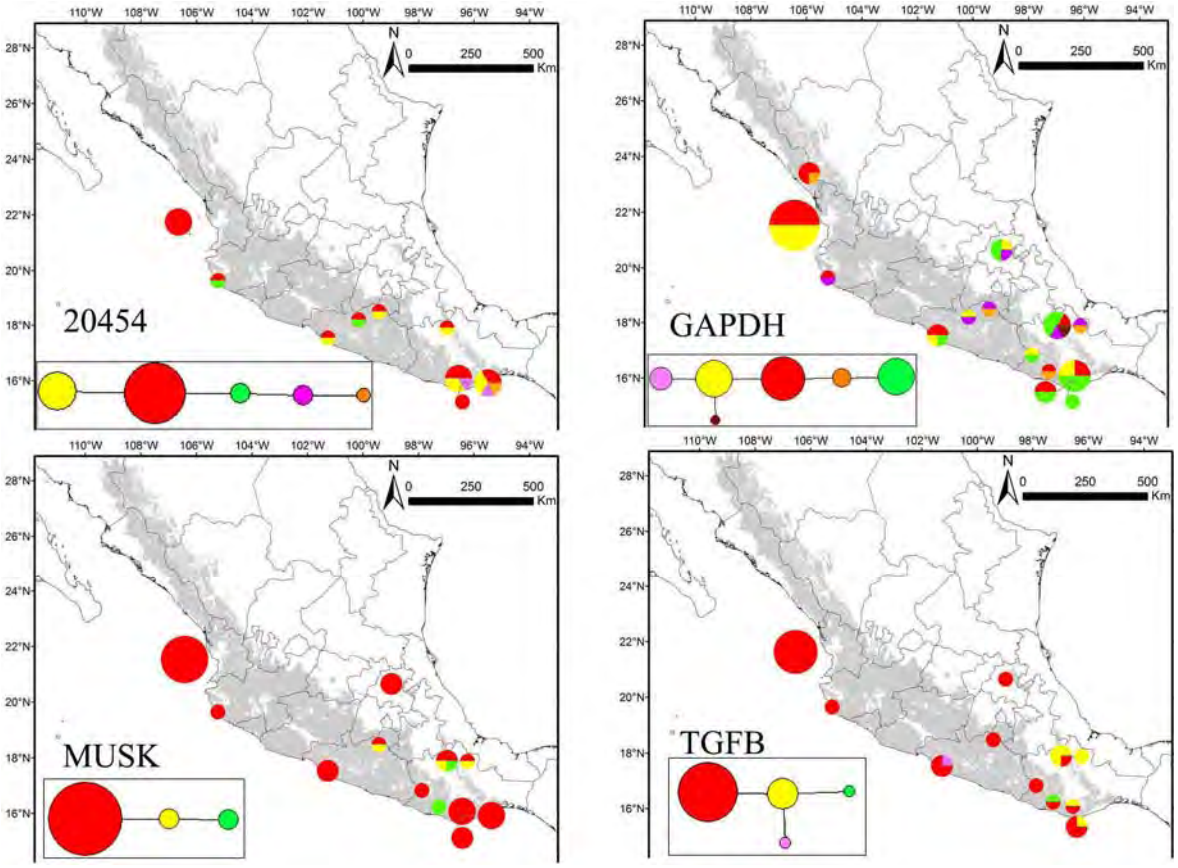


Figure 3. Scatter plot of a PCA including morphometric measurements of the Mexican endemic *Vireo hypochryseus*. Each Mexican state and the Tres Marías islands are represented with different symbol.

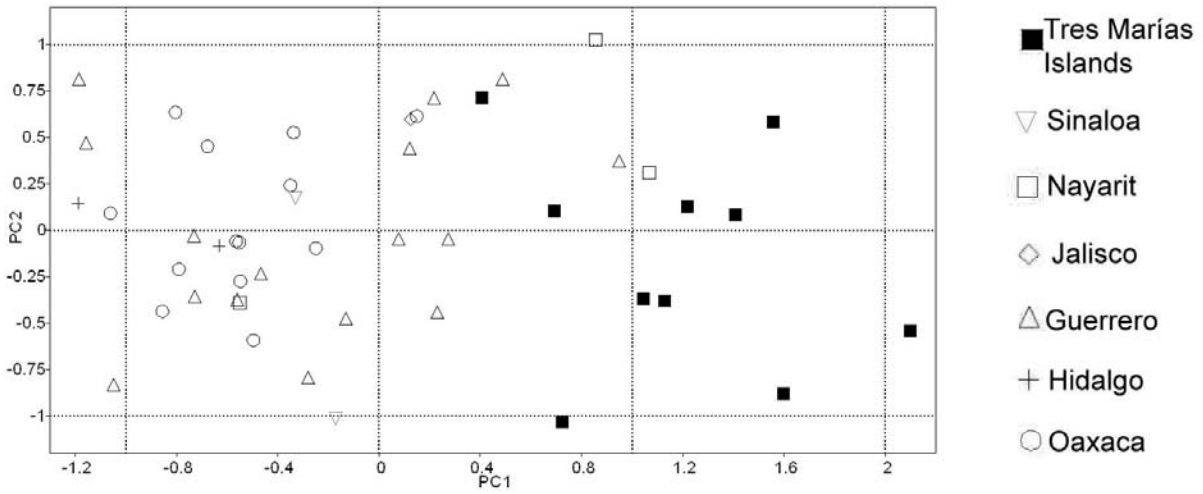


Figure 4. Box plots depicting differences in five morphometric measures between populations of *Vireo hypochryseus* in Tres Marías Islands and the mainland. Mean, standard errors and ranges of the values are depicted. Mann-Whitney test for all comparisons, except exposed culmen, were significant ($P < 0.001$).

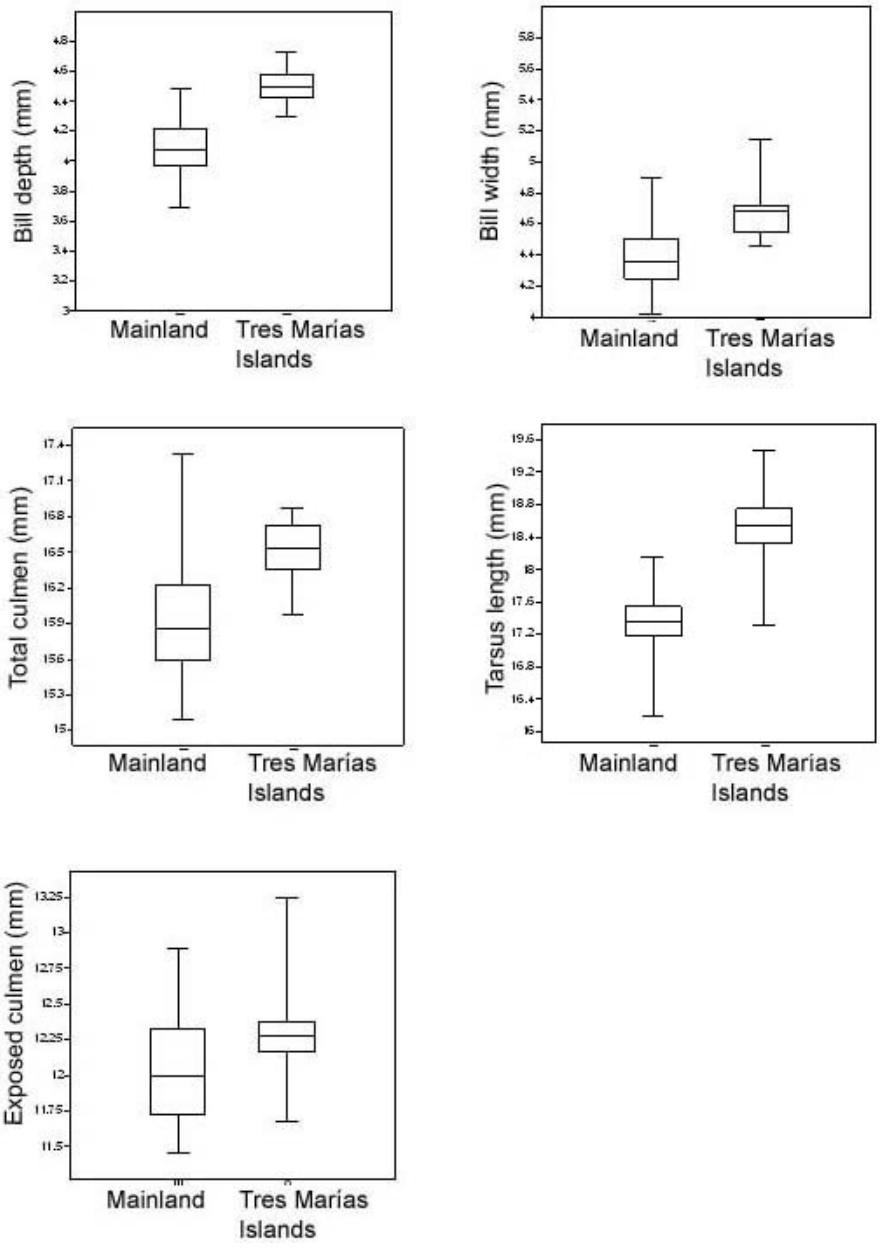
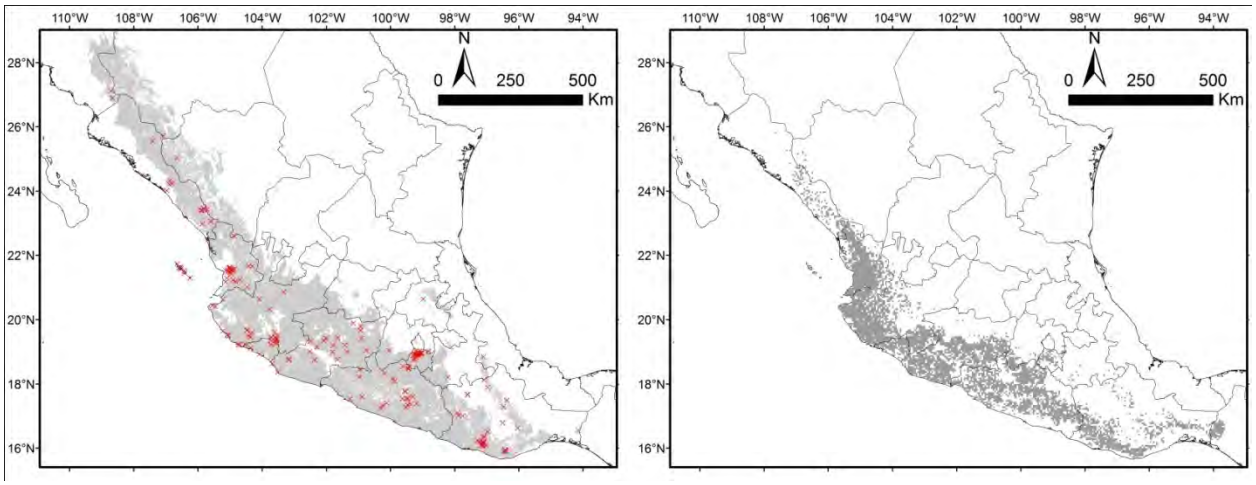


Figure 5 Left. Map depicting the actual range (grey) of *V. hypochryseus* and the localities used in the ENM (red crosses). Right. Map depicting the stable areas over the last 130 000 years for the environmental conditions where *Vireo hypochryseus* inhabits according to ENMs projected on past climatic layers.



Appendix. List of individuals of the Mexican *Vireo hypochryseus* included in this study, indicating collecting localities and GenBank accession numbers for DNA sequences (to be provided).

Collection number	State	Locality	Latitude	Longitude	ND2	20454	GAPDH	MUSK	TGFB
PLU 024	OAXACA	Pluma Hidalgo, El Carmen	15.886	-96.934	####				
AMT 342	OAXACA	Finca Soconusco a 3 km de Pluma Hidalgo, Dto. Pochutla	15.925	-96.420	####	####		####	####
AMT 351	OAXACA	Finca Soconusco a 3 km de Pluma Hidalgo, Dto. Pochutla	15.925	-96.420	####	####	####	####	####
AMT 418	OAXACA	Finca La Cruz a 1 km de Pluma Hidalgo, Dto. Pochutla	15.925	-96.420	####	####	####	####	
PLU 293	OAXACA	Pluma Hidalgo	15.927	-96.423	####		####	####	
CONACYT04 237	OAXACA	Pluma Hidalgo, Finca El Brasil	16.079	-96.557	####		####		####
CONACYT04 172	OAXACA	Pluma Hidalgo, Finca El Brasil	16.079	-96.557	####	####	####	####	
CONACYT04 199	OAXACA	Pluma Hidalgo, Finca El Brasil	16.079	-96.557	####	####	####	####	
CONACYT04 198	OAXACA	Pluma Hidalgo Finca El Brasil	16.079	-96.557	####	####	####	####	
Conacyt04 232	OAXACA	Pluma Hidalgo,Finca el Brasil	16.079	-96.557	####	####		####	

OMVP 1015	OAXACA	Distrito de Juquila, 4 km E Peñas Negras	16.237	-97.287	####		####	####	####
OMVP 699	OAXACA	Yucucino, cerca de santa Ana Progreso, Putla	16.828	-97.880	####		####	####	####
CAON 012	GUERRERO	Petatlán	17.538	-101.269	####	####	####	####	####
CAON 001	GUERRERO	Petatlán	17.538	-101.269	####		####	####	####
OMVP 0885	OAXACA	Santiago Quiotepec	17.900	-96.975	####		####	####	####
OMVP 0873	OAXACA	Santiago Quiotepec	17.900	-96.975	####		####	####	####
OMVP 0859	OAXACA	3 km SE de santiago Quiotepec	17.900	-96.975	####		####	####	####
OMVP 0886	OAXACA	Santiago Quiotepec	17.900	-96.975	####	####	####		
Inecol 53	GUERRERO	Arcelia, Campo Morado, San Rafael	18.192	-100.162	####	####	####		
UAG 024	GUERRERO	Coxcatlán	18.483	-99.425	####	####	####	####	####
FPO CHA 02	JALISCO	Bahía de Chamela, Playa Negritos	19.642	-105.225	####	####	####	####	####
AGM 086	HIDALGO	Tolantongo, Balneario Tolantongo	20.645	-98.978	####		####	####	####
AGM 088	HIDALGO	Tolantongo, Balneario Tolantongo	20.645	-98.978	####		####	####	
ITM 196	NAYARIT	Islas Marías, Isla María Magdalena, 2 do Campamento (aguada)	21.531	-106.426	####		####	####	

ITM 076	NAYARIT	Islas Marías, Isla María Magdalena, 1er Campamento (base)	21.626	-106.543	####		####	####	####
ITM 015	NAYARIT	Islas Marías, Isla María Magdalena, 1er Campamento (base)	21.626	-106.543	####		####	####	####
ITM 083	NAYARIT	Islas Marías, Isla María Magdalena, 1er Campamento (base)	21.626	-106.543	####		####	####	####
ITM 024	NAYARIT	Islas Marías, Isla María Magdalena, 1er Campamento (base)	21.626	-106.543	####		####		
ITM 181	NAYARIT	Islas Marías, Isla María Madre, campamento El Zacatal	21.740	-106.655	####	####	####	####	####
ITM 167a	NAYARIT	Islas Marías, Isla Islas Marias, Isla María Madre, campamento El Zacatal	21.740	-106.655	####	####	####	####	####
ITM 177	NAYARIT	Islas Marías, Isla María Madre, campamento El Zacatal	21.740	-106.655	####	####	####	####	####
ITM 169	NAYARIT	Islas Marías, Isla María Madre, campamento El Zacatal	21.740	-106.655	####		####	####	####
SIN 184	SINALOA	Rancho Mojocoan, 4km oeste de Copala	23.403	-105.902	####		####		
SIN 197	SINALOA	Rancho Mojocoan, 4km oeste de Copala	23.403	-105.902	####		####		

Table S1. PCR protocols used to amplify mtDNA and nDNA regions of *Vireo hypochryseus*.

Locus	Primers	PCR protocol
ND2	Lint1eac, H6313	94°C x 5 , 7 cycles (94°C x 30 sec, 60°C x 30 sec, 72°C x 1 min), 7 cycles (94°C x 30 sec, 55°C x 30 sec, 72°C x 1 min), 12 cycles (94°C x 30 sec, 52°C x 30 sec, 72°C x 1 min), 12 cycles (94°C x 30 sec, 49°C x 30 sec, 72°C x 1 min), 72°C x 10 min
ND2	eac-ND2Hint3, L5215	94°C x 5 , 7 cycles (94°C x 30 sec, 60°C x 30 sec, 72°C x 1 min), 10 cycles (94°C x 30 sec, 55°C x 45 sec, 72°C x 30 seg), 10 cycles (94°C x 30 sec, 52°C x 30 sec, 72°C x 30 seg), 20 cycles (94°C x 30 sec, 49°C x 30 sec, 72°C x 30 seg), 72°C x 10 min
ND2	H1056U, L5215U	94°C x 5 , 5 cycles (94°C x 45 sec, 55°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 53°C x 45 sec, 72°C x 1 min), 15 cycles (94°C x 45 sec, 52°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 50°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 49°C x 45 sec, 72°C x 1 min), 72°C x 10 min
ND2	eac-ND2Lin1, H1056U,	94°C x 5 , 5 cycles (94°C x 30 sec, 55°C x 30 sec, 72°C x 1 min), 5 cycles (94°C x 30 sec, 53°C x 30 sec, 72°C x 1 min), 5 cycles (94°C x 30 sec, 52°C x 30 sec, 72°C x 1 min), 10°C ycles (94°C x 30 sec, 51°C x 30 sec, 72°C x 1 min), 10 cycles (94°C x 30 sec, 50°C x 30 sec, 72°C x 1 min), 72°C x 10 min

COI	COIBirdF1, COIbirdR2	94°C x 5 min, 35 cycles (94°C x 45 seg, 53°C x 40 seg, 74°C x 45 seg), 72°C x 10 min
20454	20454F,20454R	94°C x 5 , 5 cycles (94°C x 30 sec, 52°C x 30 sec, 72°C x 1 min: 15 sec), 5 cycles (94°C x 30 sec, 51°C x 30 sec, 72°C x 1 min: 15 sec), 5 cycles (94°C x 30 sec, 50°C x 30 sec, 72°C x 1 min: 15 sec), 10 cycles (94°C x 30 sec, 49°C x 30 sec, 72°C x 1 min: 15 sec), 15 cycles (94°C x 30 sec, 48°C x 30 sec, 72°C x 1 min: 15 sec), 72°C x 10 min
GAPDH	GapdL890, GapdH950	94°C x 5 min, 5 cycles (94°C x 30 sec, 62°C x 30 sec, 72°C x 30 sec), 5 cycles (94°C x 45 sec, 61°C x 30 sec, 72°C x 30 sec), 10 cycles (94°C x 45 sec, 60°C x 30 sec, 72°C x 45 sec), 5 cycles (94°C x 30 sec, 58°C x 30 sec, 72°C x 30 sec), 10 cycles (94°C x 30 sec, 57°C x 30 sec, 72°C x 30 sec), 72°C x 10 min
MUSK	MUSK-I3F, MUSK-I3R	94°C x 5 , 5 cycles (94°C x 45 sec, 58°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 56°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 54°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 52°C x 45 sec, 72°C x 1 min), 5 cycles (94°C x 45 sec, 51°C x 45 sec, 72°C x 1 min), 15 cycles (94°C x 45 sec, 50°C x 45 sec, 72°C x 1 min), 72°C x 7min
TGFB	TGFB2.5F, TGFB2.6R	94°C x 5 min, 5 cycles (95°C x 20 sec, 55°C x 45 sec, 72°C x 1 min: 15 sec), 5 cycles (95°C x 20 sec, 54°C x 45 sec, 72°C x 1 min: 15 sec), 15 cycles (95°C x 20 sec, 50°C x 30 sec, 72°C

x 1 min: 15 sec), 10 cycles (95°C x 20 sec, 49°C x 30 sec, 72°C x 1 min: 15 sec), 10 cycles (95°C x 20 sec, 48°C x 30 sec, 72°C x 1 min: 15 sec), 72°C x 10 min

CAPÍTULO 3

Multilocus analysis of intraspecific differentiation in three endemic bird species from the northern Neotropical dry forest ☼

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Multilocus analysis of intraspecific differentiation in three endemic bird species from the northern Neotropical dry forest

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ABSTRACT

Among-species phylogeographic concordance provides insight into the common processes driving lineage divergence in a particular region. However, identifying the processes that caused phylogeographic breaks is not always straight forward, and inferring past environmental conditions in combination with documented geologic events is sometimes necessary to explain current patterns. We searched for concordant phylogeographic patterns and investigated their causes in three bird species (*Momotus mexicanus*, *Melanerpes chrysogenys*, and *Passerina leclancherii*) that belong to three different avian orders and are endemic to the northernmost range of the Neotropical dry forest. We obtained mitochondrial DNA (ND2 and COI or cyt b) and nuclear DNA (20454, GAPDH, MUSK, and TGFB) sequences for at least one locus from 162 individuals across all species and defined climatically stable areas using environmental niche model projections for the last 130,000 years to have a paleoenvironmental framework for the phy- logeographic results. All three species showed marked phylogeographic structure, with breaks found in roughly similar areas, such as the border between the Mexican states of Guerrero and Oaxaca, and between southern Jalisco and Michoacán. Both of these regions are known biogeographic breaks among other taxa. Patterns of genetic diversity and differentiation were partially compatible with climatically stable areas. Coalescent analyses revealed recent population growth and estimated the deeper haplogroup divergence of all three taxa to have occurred within the last 600,000 years. The phylogeographic patterns found are noteworthy because they are maintained in a relatively small area for bird species with continuous ranges, and highlight a unique situation when compared to phylogeographic patterns found in other studies of Neotropical birds that have stressed the role of geographic barriers to explain intraspecific differentiation. Our results point to a scenario of population isolation resulting in the present phylogeographic structure, likely a result of historical climate fluctuations that have fragmented and reconnected the Neotropical dry forest. This study contributes to a growing body of evidence indicating active diversification of endemic lineages in the northern Neotropical dry forest region.

1. Introduction

The study of geographic variation of intraspecific traits provides a window into the recent history of species. Insights into such history are detailed when phylogenetic analyses of DNA sequence data are examined in a geographic framework (i.e., phylogeography). Comparison of phylogeographic patterns across species (i.e., comparative phylogeography) provides valuable insight into the processes driving population divergence in a region (Avise, 2000). The use of multiple DNA loci of both mitochondrial and nuclear origin has been promoted to ensure the detection of patterns derived from true population-level processes rather than from locus-specific histories (Kuhner et al., 1998; Edwards and Bensch, 2009; Edwards, 2009; Manthey et al., 2011). However, the processes that have shaped phylogeographic patterns in the past are not always visible today, and paleoecological and geological information must be used to reveal the role of historical processes in intraspecific divergence (Zink, 2002; Lapointe and Rissler, 2005). An approach that combines comparative phylogeography and environmental niche modeling projected onto past climatic scenarios allows to find consensus among evidence from different sources and between methods with independent theoretical backgrounds, adding support to the chronicle of events involved in lineage divergence (Joseph et al., 1995; Schneider et al., 1998; Waltari et al., 2007; Carnaval et al., 2009; Svenning et al., 2011).

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Several studies of Neotropical birds have documented phylogeographic structure for species with discontinuous ranges due to topographical barriers that restricted gene flow and drove genetic divergence (Cadena et al., 2007; Nyári, 2007; Weir, 2009; Arbeláez-Cortés et al., 2010; Arbeláez-Cortés, 2012; Barrera-Guzmán et al., 2012; Naka et al., 2012). In these cases, the explanation of phylogeographic patterns is relatively straightforward because it is often concordant with topographical heterogeneity. In contrast, phylogeographic patterns of species with continuous ranges are heterogeneous, and have been explained by the role of past ecological changes in altering species distributions (Bates et al., 2003; Cabanne et al., 2008; Cortés-Rodríguez et al., 2008; Vázquez-Miranda et al., 2009). Moreover, species sharing distributional areas should have been influenced by similar historical processes, giving rise to concordant phylogeographic patterns (Avise, 2000; Zink, 2002; Lapointe and Rissler, 2005; Carstens and Richards, 2007; Arbeláez-Cortés, 2012).

Species endemism is not randomly distributed, and regions like Mexico host particularly high numbers of endemic bird species (Orme et al., 2006; Kier et al., 2009). Mexico holds about 100 endemic bird species, 45 of which inhabit the western Mexico ecoregion (Peterson and Navarro, 2000). Therefore, the phylogeographic patterns of western Mexican birds could be used to test whether the northern Neotropics show evidence of recent evolutionary processes driving intraspecific differentiation as has been found for other tropical regions of high endemism (Carnaval et al., 2009; Moussalli et al., 2009). Indeed, biogeographic (García-Trejo and Navarro, 2004; Espinosa et al., 2006), phylogenetic (Becerra, 2005; Becerra and Venable, 2008; De-Nova et al., 2012), and phylogeographic studies (Zaldívar-Riverón et al., 2004; Mateos, 2005; Miller and Schaal, 2005; Devitt, 2006; Mulcahy, 2008; Zarza et al., 2008; Pringle et al., 2012; Arbeláez-Cortés and Navarro-Sigüenza, 2013) have identified geographic structure in different taxonomic and geographic tiers from western Mexico. Additionally, many endemic birds of this area are composed of several subspecies (Dickinson, 2003), suggesting the existence of intraspecific variation.

The lowlands of western Mexico are bounded by the Pacific Ocean and isolated from central Mexico by the mountains of Sierra Madre del Sur and Sierra Madre Occidental (Fig. 1). The predominant ecosystem in this region is the tropical dry forest (or seasonally dry tropical forests). In fact, western Mexico encompasses the northernmost range of this highly threatened ecosystem characterized by the tree genus Bursera (Becerra, 2005; Becerra and Venable, 2008; De-Nova et al., 2012). The western Mexican tropical dry forest is continuous over extensive areas (De-Nova et al., 2012) with no apparent barriers to gene flow among populations. However, phylogeographic breaks have been found in a number of species, ranging from snakes and freshwater fishes to ants and trees, many of these breaks coinciding at the Nayarit–Jalisco and Guerrero–Oaxaca border areas (Fig. 1). The evidence of biogeographic divisions could be related to either its long and complex geological history (Morán-Zenteno et al., 2000; Devitt, 2006; Silva-Romo and Mendoza-Rosales, 2009) or to changes in its biotic communities over the last 2 million of years as a result of Pleistocene climatic fluctuations (Hubbard, 1973; Berrio et al., 2006; Ceballos et al., 2010; Lachniet et al., 2013). The high number of endemic bird species with overlapping ranges and the evidence of an active evolutionary history despite the lack of contemporary barriers to gene flow, make the northern range of the Neotropical dry forest an excellent system to search for concordant phylogeographic pattterns and find clues to the processes driving intraspecific differentiation.

Here, we compare patterns of phylogeographic structure among three bird species that are endemic to the northern Neotropical dry forest: The russet-crowned motmot (*Momotus mexicanus*), the

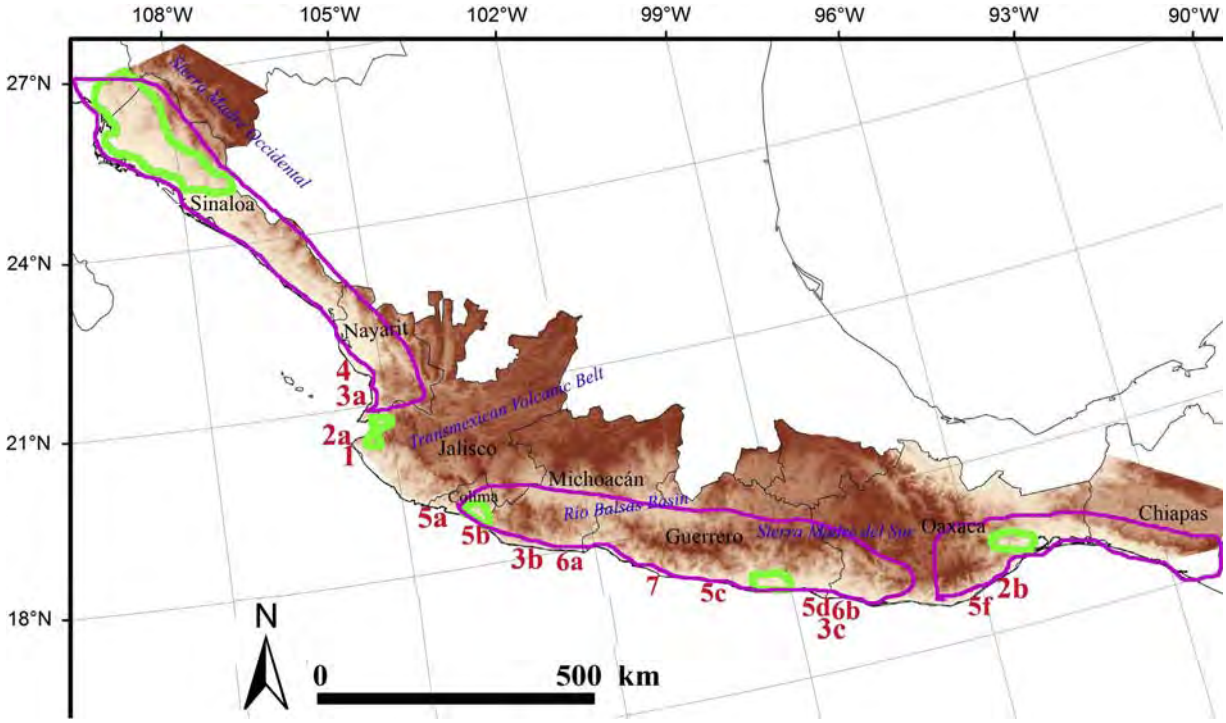

Fig. 1. Major phylogeographic breaks documented for the Western Mexico ecoregion. Numbers correspond to the approximate location of phylogeographic divisions found in the following species: 1 = the fresh water fish *Poecilia butleri* (Mateos, 2005); 2 = the frog *Rana forrieri* (Zaldívar-Riverón et al., 2004); 3 = the western lyre snake *Trimorphodon biscutatus* (Devitt, 2006); 4 = the night snake *Hypsiglena torquata* (Mulcahy, 2008); 5 = the Mexican spiny-tailed iguana *Ctenosaura pectinata* (Zarza et al., 2008); 6 = the ant *Azteca pittieri* (Pringle et al., 2012); and 7 = the tree *Spondias purpurea* (Miller and Schaal, 2005). The biogeographic areas of endemism are depicted for *Bursera* trees (Espinosa et al., 2006) and birds (García-Trejo and Navarro, 2004) by green and purple lines, respectively. Elevations above 1500 m are in dark brown, Mexican states are labeled in black, and relevant geographic areas in blue.

golden-cheeked woodpecker (*Melanerpes chrysogenys*), and the orange-breasted bunting (*Passerina leclancherii*). We determine whether phylogeographic structures are concordant among the three species and examine their intraspecific evolutionary histories in light of current geography, ecology, and historical climatic conditions. Specifically, we use a multilocus genetic dataset in a comparative phylogeographic framework to test whether: (1) there is geographically structured genetic variation in each of the three species; (2) genetic structure is spatially concordant among the three species; and (3) phylogeographic patterns are correlated with geographic and environmental distances among localities, or instead are more concordant with climatically stable areas over the last 130,000 years, a defined using environmental niche models.

2. Materials and methods

Study species, sampling and laboratory procedures

We studied three species that belong to different avian orders and are mostly endemic to western Mexico (Fig. 2): *Momotus mexicanus* (Coraciiformes: Momotidae), *Melanerpes chrysogenys* (Piciformes: Picidae), and *Passerina leclancherii* (Passeriformes: Cardinalidae). These species are relatively common in western

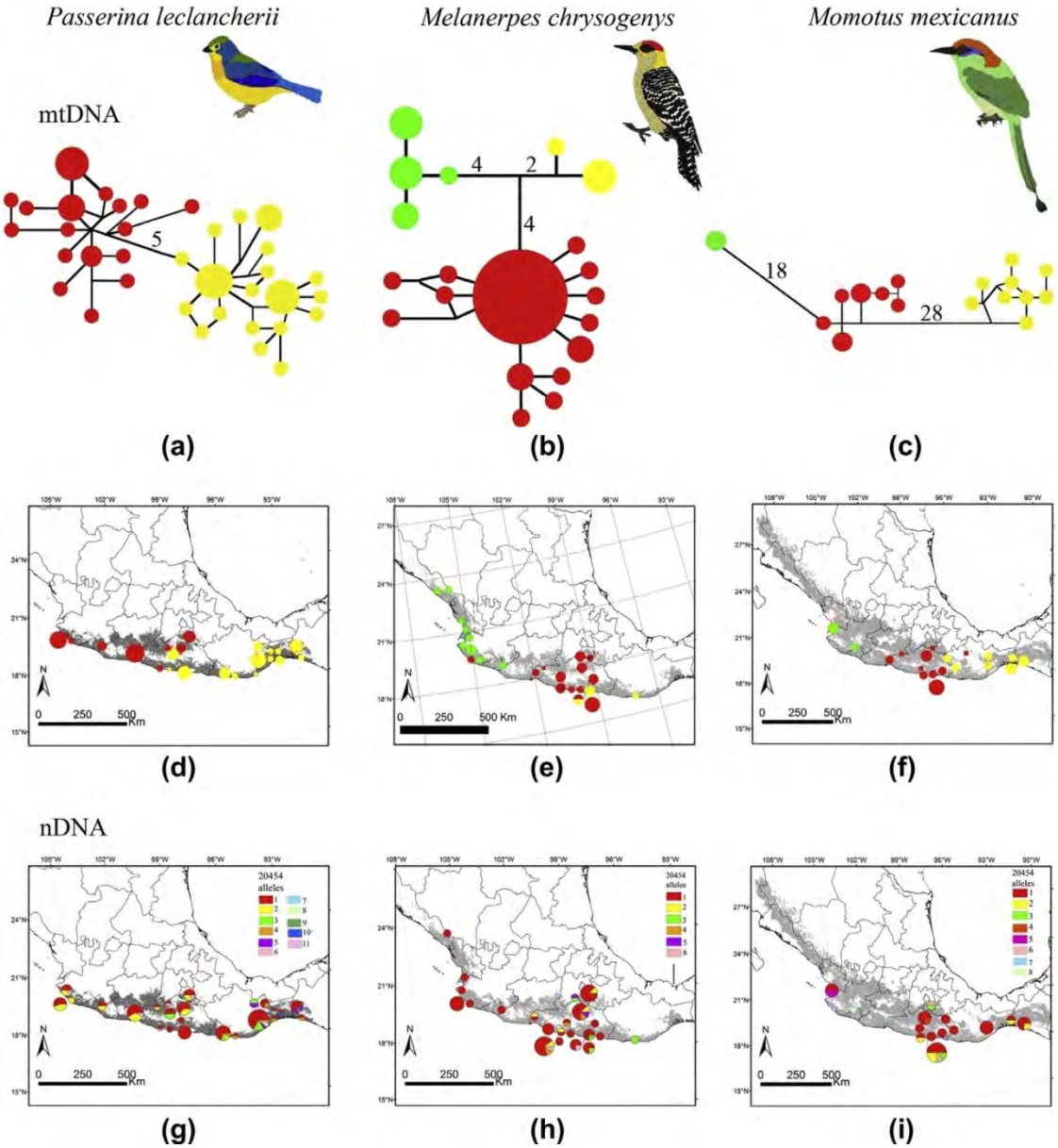

Fig. 2. Phylogeography of three bird species from the tropical dry forest of western Mexico. (a–c) Haplotype networks of the mtDNA data set. Numbers in the network edges indicate the number of mutations among major haplogroups. (d–f) Maps depict the range of each haplogroup identified in the network (same color). (g–i) Maps depicting the range of nDNA 20454 locus alleles. Circles represent haplotypes and their size is proportional to their frequency. Squares in the maps, represent samples obtained only for the COI or a short section of the ND2. Species ranges are shown in gray.

Mexico's tropical dry forest from sea level to about 1800 m, and seem to tolerate human-modified landscapes (Howell and Webb, 1995; Dickinson, 2003). *Momotus mexicanus* ranges from Sonora–Chihuahua south to western Guatemala. Samples from two subspecies (*M. m. mexicanus* and *M. m. saturatus*) were included. *Melanerpes chrysogenys* ranges from southern Sinaloa to eastern Oaxaca, including two subspecies sampled here (*M. c. chrysogenys* and *M. c. flavinuchus*). *Passerina leclancherii* ranges from Colima to south-western Chiapas encompassing two subspecies (*P. l. grandior* and *P. l. leclancherii*), both of which were sampled.

Tissue samples were obtained from field work and from the bird collection at the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC) (Additional file 1). DNA was isolated from tissues by a standard high-salt and chloroform:isoamyl alcohol method, and from small pieces of museum skins (rinsed with ethanol for 24 h) using Qiagen DNEASY™ kit (Qiagen Inc., Valencia, CA, USA) with the following modifications: 7 lL of 1 M dithiothreitol were added to the ATL buffer, and the AE buffer was diluted 1:10 and preheated to 70 ^{S}C, then used to eluted DNA in 20–50 mL.

We obtained both maternally inherited mitochondrial DNA (mtDNA) and bi-parentally inherited nuclear DNA (nDNA) sequences for each of the three species (Table 1). The nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2) was amplified using primers H6313 and L5216 or L5219 (Sorenson et al., 1999) and specific internal primers for the skin DNA samples (Additional file 2). DNA samples from museum skins were used to obtain information from localities not represented by fresh tissue samples but their data were considered only to support the general phylogeographic patterns, and not included in the remaining analyses because they yielded only short sequences. The cytochrome c oxidase subunit 1 (COI) was amplified using primers COIBirdF1 and COIBirdR2 (Hebert et al., 2004). For *P. leclancherii* we amplified the cytochrome b gene (cyt b) with primers H6313 and L5215 (Hackett, 1996). We sequenced the following nDNA loci: (1) locus 20454 using primers 20454F and 20454R (Backström et al., 2008), (2) intron 11 of glyceraldehyde-3-phosphate dehydrogenase (GAPDH), using primers GapdL890 and GapdH950 (Friesen et al., 1997), (3) muscle-specific kinase receptor intron 3 (MUSK) using primers MUSK-I3F and MUSK-I3R (Kimball et al., 2009), and (4) transforming growth factor beta 2 intron 5 (TGFB) using primers TGFB2.5F and TGFB2.6R (Sorenson et al., 2004). Two other nDNA loci (18142 and 27270; Backström et al., 2008) were tested in several samples already amplified for other loci, but failed to

Table 1. Sample sizes and diversity indices for mtDNA and nDNA datasets (obtained for three bird species from western Mexico. Diversity values include nucleotide diversity (π) and the number of haplotypes (H). The first datasets correspond to different ND2 matrices, in brackets are values for a short dataset obtained from degrades DNA from museum skin samples.

Dataset		Species		
		Passerina leclancherii	*Melanerpes chrysogenys*	*Momotus mexicanus*
ND2 (short dataset)	Aligment (bp)	660 (558)	463 (301)	579
	N, localities	59 (65), 27 (27)	46 (53), 25 (30)	28, 17
	Variable sites	27 (23)	12 (10)	32
	H	19 (18)	11 (12)	16
	p	0.006 (0.006)	0.005 (0.006)	0.017
cyt b	Aligment (bp)	737	n.a.	n.a.
	N, localities	59, 22	n.a.	n.a.
	Variable sites	32	n.a.	n.a.
	H	28	n.a.	n.a.
	p	0.006	n.a.	n.a.
COI	Aligment (bp)	n.a.	582	568
	N, localities	n.a.	45, 23	23, 15
	Variable sites	n.a.	18	33
	H	n.a.	16	11
	p	n.a.	0.005	0.023
Total mtDNA	Aligment (bp)	1395	1046	1185
	N, localities	51, 20	42, 23	21, 14
	Variable sites	52	29	67
	H	34	20	17
	p	0.005	0.005	0.02
20454	Aligment (bp)	433	433	449
	N, localities	70, 26	37, 21	21,12
	Variable sites	13	5	4
	H	13	6	7
	p	0.002	0.001	0.002
Gapdh	Aligment (bp)	295	309	335
	N, localities	19, 16	13,12	25, 15
	Variable sites	3	3	0
	H	4	4	1
	p	0.002	0.002	0
MUSK	Aligment (bp)	525	522	n.a.
	N, localities	21, 18	20, 19	n.a.
	Variable sites	3	3	n.a.
	H	3	4	n.a.
	p	0.0004	0.0009	n.a.
TGFB	Aligment (bp)	481	391	n.a.
	N, localities	20, 17	18, 17	n.a.
	Variable sites	2	2	n.a.
	H	3	3	n.a.
	p	0.0004	0.0003	n.a.

amplify. All PCR reactions were performed in 15–50 ll of volume, including 1x PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM each dNTP, 0.4–0.5 lM each primer, 1–2 unit DNA polymerase, and around 50–100 ng of DNA. PCR protocols are detailed in Additional file 3. PCR products were purified using Exo-SAP-IT™ (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA), or ethanol. The sequences were obtained by ABI Prism Bigdye™ v3.1 (Qiagen Inc., Valencia, CA, USA) terminator chemistry in an ABI 3730XL automated sequencer. Sequences were edited and aligned manually using BioEdit (Hall, 1999). For nDNA sequences we inspected chromatograms to detect double peaks, which were coded as standard IUPAC ambiguities and scanned across all individuals to check for accuracy and consistency.

Cyt b was sequenced for *P. leclancherii* instead of COI, which did not amplify in this species, and two out of the four nuclear markers (MUSK and TGFB) failed to amplify in *M. mexicanus* (Table 1). However, differences in the final genes sampled for each species are unlikely to affect our comparative analyses, as variation in cyt b and COI genes is similar in birds, and variation in MUSK and TGFB was lower among nDNA markers in *P. leclancherii* and *M. chrysogenys* (2 variable sites each), and most of the variation came from the two nDNA loci sequenced for all three species (Table 1). In all, we obtained DNA sequences from 162 individuals across all species, with number of individuals per species ranging from 33 to 76, and number of localities from 20 to 28 (Table 1 and Additional file 1). All sequences are deposited in GenBank (KC556752-KC556776, KF752719-KF753233).

Phylogenetic analyses

For each species, mtDNA regions were concatenated in a single alignment. We used these alignments to reconstruct the phylogenetic relationships among the haplotypes and to describe the phylogeographic structure of each species. Therefore we conducted four phylogenetic analyses. First, we used the program Network (Bandelt et al., 1999) to construct haplotype networks using the median-joining algorithm. To complement the phylogeographic pattern of the mtDNA, we constructed additional networks including more individuals (and localities) available for either a short region of the ND2 or the COI (Table 1). Second, we used the coalescent model in BEAST 1.7.4 (Drummond et al., 2012a,b) with a MCMC of 100,000,000 generations, sampling each 1000 generations. Third, we used the maximum likelihood method implemented in GARLI 2.0 (Zwickl, 2011) to recover phylogenetic relationships and obtain a nonparametric bootstrap support value for the nodes. Individual solutions were selected after 20,000 generations with no significant improvement in likelihood (>0.01). Solutions were selected when the total improvement in likelihood score was 0.05. We performed 100 bootstrap replicates, each including 10 independent runs. Fourth, Bayesian inference (BI) was implemented to obtain a phylogenetic reconstruction and posterior probability values as implemented in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003). We used two parallel runs, one 'cold' and three 'hot' chains for 10,000,000 generations, sampling every 1000 generations. Data were partitioned by mtDNA region and analyzed under the best-fit model for each one, selected using Akaike's information criterion in MrModeltest (Nylander, 2004). A 25% burn-in was used, and a majority rule consensus tree was calculated. In each phylogenetic analysis sequences of the congeners *Momotus momota*, *Melanerpes carolinus*, and *Passerina versicolor* were used as outgroups (Additional file 1). We used Tracer 1.5 (Rambaut and Drummond, 2009) to assess chain convergence, to determine that our sampling of the posterior distribution of the likelihoods had reached a sufficient effective sample size (ESS), and to ascertain that the posterior distribution had reached stationarity. To asses phylogeographic structure we conducted a visual inspection of the phylogenetic patterns across geographic space.

The allele phase of each nDNA locus was resolved using the coalescent-based Bayesian method of the Phase algorithm (Stephens et al., 2001; Stephens and Donnelly, 2003) in DnaSP v.5 (Librado and Rozas, 2009) employing 10,000 iterations, 10 thinning intervals, 1000 burn-in, allowing for recombination, and setting an output probability threshold of 0.9. We used the resulting highest-probability haplotypes for further analyses. Genetic diversity was measured as the number of variable sites, number of haplotypes (H), and nucleotide diversity (π) for every locus using DnaSP v.5 (Librado and Rozas, 2009).

Genetic landscape analysis

We used Landscape Genetics GIS Toolbox (Vandergast et al., 2010) in ArcGis 9.3 (ESRI, 2009) to create geographical landscapes of both genetic divergence and genetic diversity. This analysis allows a more straightforward comparison among species and provides a frame to compare genetic results with other continuous spatial results such as climatically stable areas (see below) and to gain information about spatial patterns that could be hindered when only the local values of diversity or pairwise genetic divergence are reported. For this analysis, we used K2P distances calculated in MEGA 5 (Tamura et al., 2011) among pairs of individuals, for both mtDNA and nDNA 20454, as the genetic divergence. Genetic diversity landscapes were generated by calculating the nucleotide values (p) for all localities with two or more samples (except for *M. mexicanus* due to the low number of samples per locality). Localities with just one sample were grouped with other localities within 40 km, excluding those that were farther. After scaling the raster layer values between 0 and 1, we defined the sum of both mtDNA and nDNA layers as the genetic divergence or genetic diversity landscape of each species. The continuous values obtained were classified in five categories. This analysis allows a more straightforward comparison among species and provides a framework for comparing genetic results with climatically stable areas (see below).

SAMOVA and structure analyses

To explicitly test for phylogeographic structure in each species we used Spatial Analysis of Molecular Variance in SAMOVA 1.0 (Dupanloup et al., 2002) and K2P distances among mtDNA sequences to detect major genetic discontinuities among sampling localities of each species. This method maximizes the proportion of genetic variance due to differences between a user-defined number of groups (K), and assigns localities to groups, considering that they must be geographically adjacent and genetically homogeneous (Dupanloup et al., 2002). We used K = 2 to K = 5, and calculated statistical significance with 1000 permutations.

Population structure was also assessed with Structure 2.3.1 (Pritchard et al., 2000; Pritchard et al., 2010) using the allele frequency of the nuclear markers only. We used the admixture model, with the model of correlated allele frequencies, using an MCMC of 500,000 generations burn-in and 5,000,000 total generations. We included only individuals with all the nuclear loci sequenced for *P. leclancherii* (N = 18) and all the individuals with three or more nuclear loci sequenced for *M. chrysogenys* (N = 19). We indicated the program the number of clusters expected considering the number of mtDNA haplogroups found for each species.

Congruence among distance matrices

To assess the effect of geographic and environmental (i.e. resistance) distances among sampled localities and the genetic differences among individuals from those localities, and to compare the genetic differences obtained from the mtDNA and the nDNA locus 20454 we used an analysis of Congruence Among Distance Matrices (CADM, Legendre and Lapointe, 2004), implemented in R (R Development Core Team, 2012) by using APE 2.5-2 (Paradis et al., 2004). This analysis tests whether several matrices (nDNA 20454 locus and mtDNA F_{ST} values and geographic/environmental

distances) are congruent. First, we tested for a correlation between pairwise F_{ST} values and either the geographic or the environmental distance among sampled localities, which would suggest a role of current factors in driving divergence. The absence of a significant correlation would imply the role of historical processes that are not necessarily apparent at present. Secondly, if historical processes in western Mexico influenced the biotic communities, then we expect to observe some concordance among the geographic structure found across loci and across species. Pairwise F_{ST} values were calculated in DnaSP (Librado and Rozas, 2009) among localities with two or more individuals and standardized, between 0 and 1, before analysis. Localities with few samples were grouped with other localities within 40 km, excluding those single-sample localities that were farther. First, a global test was performed for overall congruence among the matrices. When the null hypothesis of incongruence was rejected, a posteriori pair-wise CADM and one-tailed Mantel tests were conducted to identify which combinations of matrices were congruent. We used 999 permutations to assess significance and the Holm correction for multiple comparisons. First, we conducted a CADM for the samples of *M. chrysogenys* and *P. leclancherii*, independently, to search for congruence among genetic distances (mtDNA and nDNA 20457), geographic distance (linear distance in km) and 'environmental' distance (i.e., resistance distance) among localities. The resistance distance was calculated using the method proposed by McRae (2006), which estimates values of resistance among localities considering a user-defined 'resistance' layer. In this case the 'resistance' layer that we used was the inverse of an Environmental Niche Model developed in Maxent (see below) that was obtained using the raster calculator in ArcGis 9.3 (1-Maxentmodel). The original Maxent layer presented values for each pixel that could be interpreted as the probability of occurrence of the conditions where the species inhabits, therefore their inverse have higher values (i.e., high resistance) for those zones where the species did not occur. The resistance distances were calculated independently for the localities of *P. leclancherii* and *M. chrysogenys*, using the software Circuitscape 3.5.1 (Shah and McRae, 2008). Geographic and resistance distances are conceptually different, because the former assume spatial homogeneity and only one way to connect pairs of localities, while the latter take into account landscape heterogeneity and multiple ways to connect pairs of localities. Both the geographic and resistance distances were standardized, between 0 and 1, before the CADM.

The second CADM was conducted to test for congruence among the patterns of both species combining their F_{ST} matrices. However, because CADM contrasts the same units (e.g., localities) we defined four regional groups (Additional file 4) for which there were samples of both species. Therefore, this second analysis was restricted to the overlapping ranges of both species, so four F_{ST} matrices were contrasted (two for each species).

Demographic analysis and time frame of the major phylogeographic divisions

In the absence of geographical criteria to delineate populations in these continuous-range species, we grouped samples according to the major haplogroups obtained in the networks and in the BEAST analysis, which showed marked geographic structure. Therefore, samples of *P. leclancherii* were divided into two groups that also represent geographic groups: southeast Chiapas to central Guerrero) and northwest (central Guerrero to Jalisco); samples of *M. chrysogenys* were divided into three groups that also correspond to geographic groups: southeast (Oaxaca–Guerrero), central (Guerrero–Jalisco) and northwest (Jalisco–Sinaloa); finally, in *M. mexicanus* samples were divided into three groups, southeast (Chiapas–Oaxaca), central (Guerrero), and northern (Nayarit). We included only the individuals sampled for mtDNA regions that could be assigned to some of the haplogroups, therefore a few samples obtained only for nDNA markers were not used here. We calculated the population growth parameter g and parameter θ (the product of the effective population size Ne and mutation rate μ) for each haplogroup in Lamarc 2.1.6 (Kuhner, 2006), using the independent information of the mtDNA dataset and the phased alleles of each nDNA loci. We considered the appropriate substitution model of every sequence, and a mutation rate of 1:10 between nDNA and mtDNA datasets. The GAPDH locus was excluded for *M. mexicanus* due to a lack of variation, and the two individuals from Nayarit that form a different haplogroup were excluded because two samples are insufficient for this analysis. The Lamarc likelihood analysis was run with four independent chains and a sample strategy of 20 initial chains of 1000 genealogies, recorded every 40 iterations, a burn-in of 2000, and two final chains of 20,000 genealogies sampled every 40 iterations with a burn-in of 2000. The acknowledged upward bias in estimates of g (Kuhner et al., 1998) drove us to consider g values indicating demographic expansions only when positive values within 95% confidence intervals were observed. We used Tracer 1.5 (Rambaut and Drummond, 2009) to assess chain convergence and determine ESS values.

We used *BEAST (Heled and Drummond, 2010) in BEAST 1.7.4 (Drummond et al., 2012a) to calculate divergence times among haplogroups within each species independently. *BEAST implements an algorithm to construct species trees, however in our case we have not species as terminals but haplogroups or intraspecific lineages. However, our aim in implementing this analysis is to set a temporal frame for the intraspecific differentiation in each species considering the evidence of all loci sampled in order to diminish the variation associated to values calculated from a single DNA marker. Therefore, we included the mtDNA haplotypes and nDNA alleles (phased) for all loci evaluated in each species. This non-concatenated dataset allowed us to use the complete information obtained for each species (except the GAPDH of *M. mexicanus*, which was not variable). For each species and dataset we ran the analyses for 100,000,000 steps, sampling every 1000 steps, using a Yule speciation tree prior, a UPGMA starting tree, a log normal relaxed uncorrelated molecular clock, 2.9×10^{-8} substitutions/site/year for ND2, 2.07×10^{-8} substitutions/site/year for cyt b, 1.6×10^{-8} substitutions/site/year for COI, 1.67×10^{-9} substitutions/site/year for the 20454, 1.2×10^{-9} substitutions/site/year for GAPDH, and 1.7×10^{-9} substitutions/site/year for TGFB and MUSK, according to rates reported previously for those or for similar genes in birds (Weir and Schluter, 2008; Smith and Klicka, 2010; Lerner et al., 2011; Lim and Sheldon, 2011; Manthey et al., 2011; Sly et al., 2011). After the analysis we used TreeAnnotator v1.7.4 (Rambaut and Drummond, 2012) to generate a tree-file compiling the data, using a 25% burn-in, and a posterior probability limit of 0.5. We used Tracer 1.5 (Rambaut and Drummond, 2009) to determine the ESS. We tested for recombination in the nuclear loci using the Four Gamete Test in DnaSP v.5 (Librado and Rozas, 2009).

Definition of climatic stable areas through environmental niche models (ENM)

We constructed ENM with data for the present and projected them onto one present and two past environmental scenarios to define climatic stable areas. We included 19 bioclimatic variables from WorldClim (Hijmans et al., 2005) and three topographic layers from the Earth Resources Observation and Science Center (2011). The paleoenvironmental layers were drawn from the general circulation model simulations from the Community Climate System Model and the Model for Interdisciplinary Research on Climate for the Last Glacial Maximum (21,000 years ago) and the Last Interglacial Period (130,000 years ago). The bioclimatic layers were the ones available at WorldClim Global Climate Data Version 1.4 (2012).

Georeferenced localities were gathered from the Atlas de las aves de México database (Navarro et al., 2003), for a total of 239 localities for *P. leclancherii*, 354 for *M. chrysogenys*, and 454 for *M. mexicanus*. For each species, the layers were clipped with a polygon around the localities plus a 50-km buffer. To use only uncorrelated layers, we extracted the environmental data of every locality and correlated them among layers using PAST (Hammer et al., 2001), excluding one of every pair of layers with $r > 0.9$. Both GARP (Anderson et al., 2003) and Maxent (Phillips et al., 2006) were used. Both algorithms have been used to transfer niche space into past scenarios (Waltari et al., 2007; Carnaval et al., 2009; Svenning et al., 2011), and have received variable support concerning their performance (Elith et al., 2006; Peterson et al., 2007; Peterson et al., 2008). GARP with best subsets was conducted in openModeller 1.1 (Muñoz et al., 2009) with 100 runs, a maximum number of iterations = 800, and selecting the 10 best models out of 100. Maxent was run for ten replicates in Maxent 3.3 (Phillips et al., 2006) using cross-validation and without clamping in the projections. For GARP, we determined the 10% of the localities with the lower values according to the model projected onto the present, and the maximum value of that 10% was set as the presence–absence logistic threshold of the test omission rate closer to 10%. Such thresholds were then applied to the projections in the palaeocli- matic layers. We defined climatic stable areas (e.g., Carnaval et al., 2009) along the last 130,000 years by multiplying the pre- dicted presence–absence maps (pixel values of 1 and 0) for each algorithm using the Raster calculator of ArcGis 9.3. Then we selected the areas where both algorithms coincided. For Maxent, we selected the best of the models using Partial ROC (Barve, 2008) with 50% points in bootstrap, 1000 resampling, and 0.9 of 1-omission threshold. Once the best model was selected, we defined presence–absence values by selecting the the logistic threshold of the test omission rate closer to 10%. Such thresholds were then applied to the projections in the palaeoclimatic layers. We defined climatic stable areas (e.g., Carnaval et al., 2009) along the last 130,000 years by multiplying the predicted presence–absence maps (pixel values of 1 and 0) for each algorithm using the Raster calculator of ArcGis 9.3. Then we selected the areas where both algorithms coincided.

3. Results

Phylogeographic patterns and genetic diversity

We found phylogeographic structure for the mtDNA of each species, which presented breaks in roughly the same areas (Fig. 2–c). Phylogeographic patterns were identified based on mtDNA networks (Fig. 2) and were supported by the spatial distribution and frequency of some nDNA alleles (Fig. 3), by the coalescent based tree in BEAST (Fig. 4), and partially by BI and ML topologies (Fig. 4), genetic divergence landscapes (Fig. 5), and SAMOVA (Additional file 5). All ESS values were above 1500 for the BI and BEAST analyses.

For *P. leclancherii* we found two mtDNA haplogroups differentiated by five mutations (Figs. 2a, d and 4), representing 0.36% of the sequence analyzed. One of the haplogroups (south-eastern) ranges from western Chiapas to central Guerrero, and the other one (north-western) extends from Jalisco east into the Balsas Basin and along the coast to central Guerrero. The short ND2 sequence dataset (Fig. 2) supports this pattern by assigning three samples from Chiapas–Oaxaca and Guerrero coast to the south-eastern haplogroup, and two samples of the Balsas Basin in Guerrero to the north-western haplogroup. Even though the coalescent tree supported both haplogroups as clades (posterior probability values >0.96) the BI and ML topologies only agree partially with such re- sults.

The BI supported the north-western (posterior probability value = 0.8), but not the south-eastern clade, which resulted in paraphyletic relationships among haplotypes. In contrast, the non-parametric bootstrap of the ML analysis supported only the south-eastern haplogroups (bootstrap = 55) while the haplotypes from the north-western haplogroup conformed a polytomy. The CADM comparing mtDNA and nDNA 20454 locus indicated that their F_{ST} matrices were congruent (Mantel correlation = 0.62, P = 0.001). Although the Structure analysis of the nDNA loci did not show evidence of genetic structure in the individual genotypes, slight differences in the geographic distribution of alleles were detected. For example, some alleles of the 20454 locus (Fig. 2g) were largely restricted to specific areas similar to the ranges of the mtDNA haplogroups. The most common allele of the 20454 locus (allele 1) was spread across the entire *P. leclancherii* range, but other alleles were mostly restricted to specific areas similar to the ranges of the mtDNA haplogroups. This is the case of allele 3, found mainly from Jalisco to Morelos, while from Chiapas to Oaxaca two frequent alleles (4 and 2) were observed. The TGFB and MUSK introns also seemed to show differences in the distribution of their alleles (Fig. 3c and e) in spite of the limited sample sizes. For both of them, the rare alleles (2 and 3) are almost restricted to individuals from one mtDNA haplogroup, yet the common allele (1) is widespread.

For *M. chrysogenys* we defined three haplogroups separated by six or eight mutations (Figs. 2b, e, and 4), which correspond to 0.6–0.8% of the mtDNA analyzed. Individuals from the southeast (eastern Guerrero to Oaxaca) corresponded to one haplogroup, while individuals from the central range (Morelos to eastern Guerrero) and two from Jalisco correspond to a separate haplogroup. A third haplogroup includes individuals spanning the north-western part of the range (Sinaloa to Michoacán), except for the two individuals from the central haplogroup found in Jalisco. This haplogroup definition was supported by additional samples from the short ND2 sequence dataset and single sequences obtained for COI (Fig. 2). Six samples of the short ND2 sequence dataset and three COI sequences from Guerrero and Morelos corresponded to the central haplogroup, while another ND2 short sequence from Nayarit was grouped with samples from the north-western range. The three haplogroups were supported by the posterior probability values of the coalescent analysis (>0.98) but only the south east and central haplogroups were partially supported by both ML (bootstrap values >50) and BI (posterior probability values >0.6) while the north-western haplogroup exhibited a BI posterior probability support of just 0.5 and was a polytomy in the ML analysis. Structure analysis of the nDNA loci did not show evidence of genetic structure in the individual genotypes. However, the 20454 nDNA locus presented some spatial structure, showing a widespread allele (allele 1, Fig. 2h), that is also the only one found in individuals from Sinaloa to Michoacán; while five additional alleles were present in the south-eastern samples (Fig. 2h). The alleles of GAPDH and MUSK also showed some geographical differences (Fig. 3b and d). The GAPDH allele 2 was present only in individuals from the north and the Balsas basin while the widespread allele 1 was frequent in individuals from Guerrero and Oaxaca. Moreover, MUSK allele 3 was exclusive for the northernmost individuals (from Sinaloa), allele 2 was present only in samples from Nayarit, Jalisco, and the Balsas basin; while allele 4 was restricted to individuals in eastern Guerrero. In this species some localities shared mtDNA haplotypes belonging to different haplogroups, indicating the existence of population-level admixture. However these 'mixed' localities in Jalisco and Guerrero are in contact areas among haplogroups (Fig. 2e). The mtDNA phylogeographic structure of *M. mexicanus* showed three haplogroups differentiated

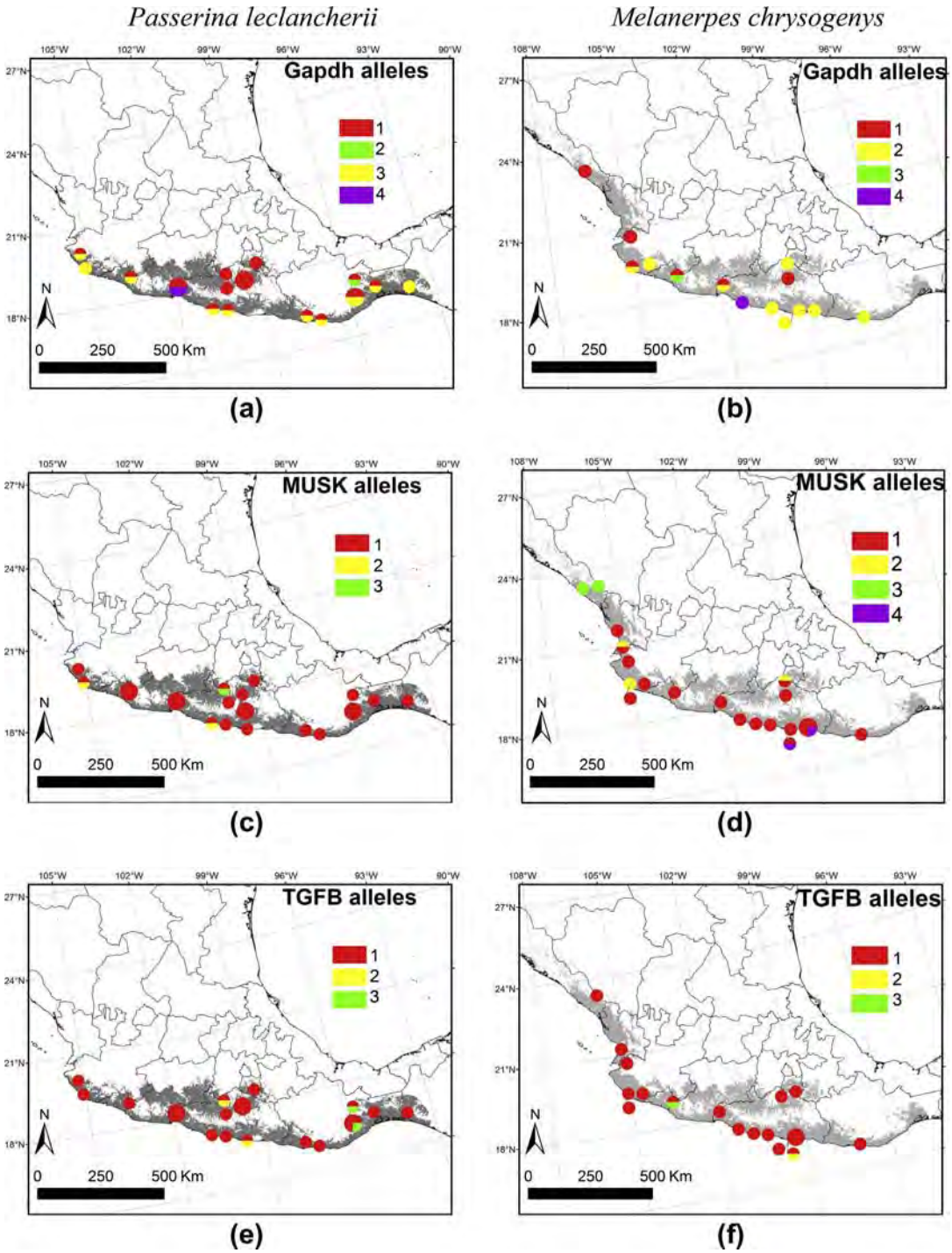

Fig. 3. Range of the alleles of three nDNA introns of two bird species endemic to western Mexico. (a and b) GAPDH, (c and d) MUSK, and (e and f) TGFB. Circles size is proportional to samples frequency. Species ranges are shown in gray.

by 18 and 46 mutations (Fig. 2c, f, and 4), which corresponds to 1.5–3.9% sequence divergence among clades. One haplogroup was restricted to the southeast (Chiapas– Oaxaca), another to the central region (Guerrero), and two individuals from Nayarit formed a third haplogroup. Additional sequences obtained for only one mtDNA marker (ND2 short dataset or only COI, Fig. 2) supported this haplogroup structure, including localities in Guerrero and Morelos in the central haplogroup, and one sample from Nayarit and two samples from southern Jalisco in the northern haplogroup. One individual from Cuicatlán Valley (W 97°, N 17.6°) in Oaxaca, sequenced only for COI, presented one haplotype of the central haplogroup. This valley is connected to the Balsas Basin (where the central haplogroup dominates) by areas below 1900 m in elevation, but is separated from the Oaxaca coast (where the south-eastern haplogroup is dominant) by higher elevations. The three haplogroups were also supported by the coalescent and BI trees (all posterior probability values = 1). However, the ML bootstrap value for the south eastern haplogroup was only 54 and the central haplogroup was not supported. In contrast to the mtDNA structure of *M. mexicanus*, all the sequences obtained for the GAPDH were invariable (Table 1). Genetic diversity varied among species and datasets (Table 1). Nucleotide diversity (p) varied between 0.0003 and 0.002 for nDNA

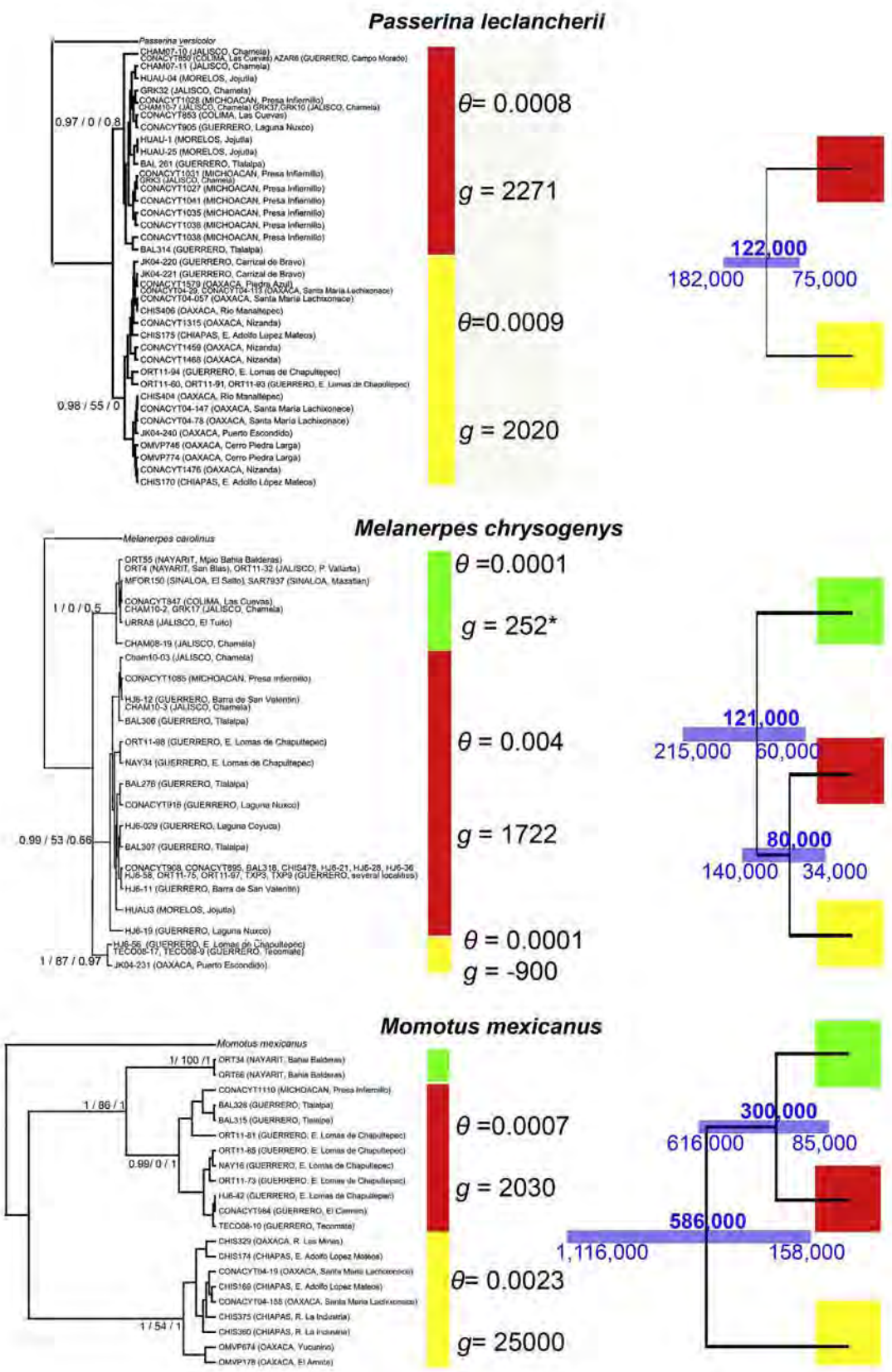

Fig. 4. Coalescent tree for three bird species endemic to western Mexico based on mtDNA data. Support for each major clade according to different analyses are indicated in the following order: coalescent tree posterior probability values/ML bootstrap/BI posterior probability values. Time divergence estimates in years (HPD and 95% confidence interval, *BEAST). Colors besides the trees depict the haplogroups from Fig. 2. The demographic values θ (the product of the effective population size Ne and mutation rate μ) and g (a population growth parameter) calculated in Lamarc are indicated for each haplogroup. *depicts a positive g value that has negative values within their 95% confidence interval.

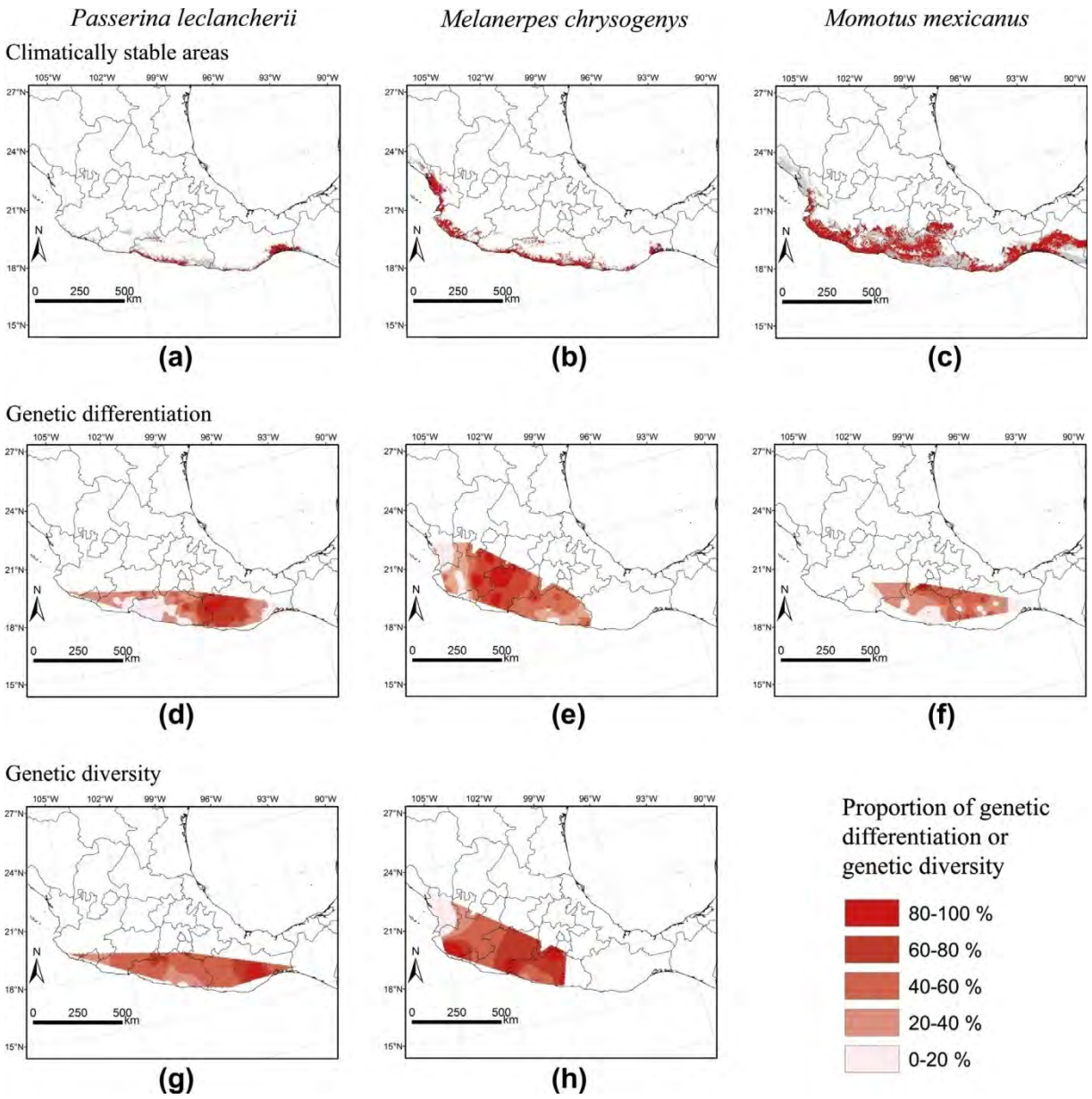

Fig. 5. Maps of climatic stable areas and genetic landscapes of three bird species from western Mexico. (a–c) Climatic stable areas during the last 130,000 years as determined using ENM projected under three temporal scenarios. Red areas are thosewhere both Maxent and GARP coincided in their predictions, while gray areas are those where only one method made a prediction. (d–f) Geographic landscapes of genetic differentiation. (g and h) Genetic diversity landscapes classified in five groups and depicted in different red tones. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and between 0.005 and 0.006 for mtDNA of *P. leclancherii* and *M. chrysogenys*, but was one order of magnitude higher for *M. mexicanus* mtDNA (0.016–0.023) although nDNA diversity of this species was low (0 and 0.002) (Table 1).

Spatial analyses of genetic variation

For *P. leclancherii* and *M. mexicanus* the genetic landscapes (Fig. 5) showed zones of relatively large genetic divergence be- tween Guerrero and Oaxaca (around W 98°, N 17°); while for *M. chrysogenys* it was between Michoacán and Jalisco (around W 102.7°, N 19.5°). The SAMOVA also indicated that a majority of breaks occurred near those zones (Additional file 5). For *P. leclancherii*, K = 2 grouped samples in a similar way to their haplogroups (Fig. 2d and Additional file 5). For *M. mexicanus* and *M. chrysogenys* K = 2 and K = 3 divided the samples in accordance to major haplogroups (Fig. 2e, f and Additional file 5).

Therefore, as a general result, both SAMOVA and genetic divergence landscape indicated that the major phylogeographic division of *P. leclancherii* and *M. mexicanus* and a secondary break for *M. chrysogenys* are in the southeast (around the Oaxaca–Guerrero boundary); while the major phylogeographic division of *M. chrysogenys* is in the northwest (Michoacán–Jalisco), coinciding roughly with the second division found for *M. mexicanus*. Additionally, *Passerina leclancherii* showed one zone of high diversity in central Oaxaca while *M. chrysogenys* showed four regions: two along the coast and two in the Balsas Basin (Fig. 5). This analysis was not conducted for *M. mexicanus*, but central Guerrero seems to harbour high genetic diversity (nDN 20454, Fig. 2i). As mentioned above, the Structure analyses of the nDNA loci did not show evidence of genetic structure in the individual genotypes of *P. leclancherii* and *M. chrysogenys*. In this analysis each individual was assigned to each predefined group with the same probability

Table 2 Congruence among distance matrix (CADM) results. Test for congruence among F_{ST} values (mtDNA and 20457 locus) and geographic and resistance distances. CADM for the samples of *M. chrysogenys* and *P. leclancherii* (per locality dataset, left). CADM to test for congruence among both species (pooled dataset, right). Results of the global test (a priori) are above and results of a posteriori pair-wise test are below.

A priori CADM H_0: matrices are incongruent	Per locality dataset: *Passerina leclancherii* (mtDNA F_{ST} × 20454 F_{ST} × geographic × resitance distances) 12 localities	*Melanerpes chrysogenys* (mtDNA F_{ST} × 20454 F_{ST} × geographic × resistance distances) 9 localities	Pooled localities dataset (*P. leclancherii* mtDNA F_{ST} × 20454 F_{ST}) × (*M. chrysogenys* mtDNA F_{ST} × 25454 F_{ST}) 4 regional groups
Kendall's W	0.646	0.739	0.05
Friedman's X^2	168.025, P = 0.001	103.433, P = 0.001	1, P = 0.965

A posteriori CADM Pairwise congruence H_0: matrix is incongruent with remaining matrices

	P-value	Adjusted *P*-value
mtDNA	0.001	0.004
20454	0.001	0.004
Geographic distance	0.001	0.004
Resistance distance	0.001	0.004

	P-value	Adjusted *P*-value
mtDNA	0.1	0.4
20454	0.1	0.4
Geographic distance	0.1	0.4
Resistance distance	0.1	0.4

One-tailed Mantel tests H_0: r = 0

	Mantel cor.	*P*-value
mtDNA x 20454	0.62	0.001
mtDNA x Geographic distance	0.52	0.003
20454 x Geographic distance	0.24	0.075
mtDNA x Resistance distance	0.54	0.002
20454 x Resistance distance	0.31	0.018
Geographic x Resistance distance	0.93	0.001

	Mantel cor.	*P*-value
mtDNA x 20454	0.36	0.1
mtDNA x Geographic distance	0.67	0.1
20454 x Geographic distance	0.51	0.1
mtDNA x Resistance distance	0.78	0.1
20454 x Resistance distance	0.53	0.2
Geographic x Resistance distance	0.97	0.1

(around 0.5 for *P. leclancherii* and around 0.33 for *M. chrysogenys*). We think that low sequence variation in nDNA markers is a more parsimonious explanation than gene flow for this pattern, but more variable markers will have to be analyzed.

The global CADM performed to compare F_{ST} matrices of mtDNA and locus 20454 and matrices of geographic and resistance distances rejected the null hypothesis of incongruence among matrices (Table 2), and the a posteriori CADM showed that each matrix is congruent with at least another matrix. The major correlation was found between geographic and resistance distances in both species (Mantel correlation >0.9), but was not significant for *M. chrysogenys*. As mentioned above the mtDNA and nDNA F_{ST} of *P. leclancherii* were correlated while those genetic matrices were not congruent in *M. chrysogenys*. In *P. leclancherii* the mtDNA F_{ST} showed a significant correlation with both geographic and resistance distances (Mantel correlation: 0.52 and 0.54). The nDNA 20454 locus of this species only showed a lower (Mantel correlation: 0.31) but signif- icant (P < 0.05) correlation with the resistance distance. Although the congruence among matrices found for *M. chrysogenys* was not significant at α = 0.05, the mtDNA F_{ST} seems to be related with geographic and resistance distances (Mantel correlation >0.6, Table 2), being more correlated with the second one (Mantel correlation = 0.78). The global CADM used to contrast the matrices of both species indicated that the matrices were incongruent, suggesting that both species have different spatial genetic structure or that our regional grouping scheme was inadequate to detect congruence among them.

Historical demography and divergence time

The g parameter indicated a trend of population growth for the haplogroups of *P. leclancherii* and *M. mexicanus* and for the central haplogroup of *M. chrysogenys* (Fig. 4). The north-western group of haplogroup presented negative values of g. The majority of ESS values were major than 300 for all loci and species. However, some loci such as MUSK of one haplogroup of *P. leclancherii* and 20454 for one haplogroup of *M. chrysogenys* were below 200 despite the longer runs used in the Lamarc analyses. This could be caused by the low variation of these loci in such populations. *BEAST analysis (Fig. 4) set a time frame for the occurrence of the division among haplogroups of the three species during the Pleistocene, with high posterior probability values during the last 586,000 years, and confidence intervals back to 1,116,000 years ago in the deepest divergence among haplogroups of *M. mexicanus*. All ESS values were above 300.

Climatic stable areas

ENM predicted accurately the range of each species (AUC values: *P. leclancherii* = 0.77 and 0.88, *M. chrysogenys* = 0.72 and 0.85, and *M. mexicanus* = 0.74 and 0.79; for GARP and Maxent, respectively). The climatic stable areas were small in comparison with present species ranges (Fig. 5), and were more or less discontinuous. For *P. leclancherii* (Fig. 5a) two climatic stable areas were defined (Oaxaca close to the Isthmus of Tehuantepec and Guerrero coast). Those areas were on both sides of the maximum genetic divergence zone (Fig. 5d) and were partially concordant with the range of the two major mtDNA haplogroups. Another noteworthy pattern is the concordance between the Oaxaca stable area and the high genetic diversity zone (Fig. 5g). *Melanerpes chrysogenys* presented three climatically stable areas in Oaxaca (Fig. 5b), the westernmost showing geographic concordance with that of *P. leclancherii*. From eastern Guerrero to northern Nayarit runs a strip characterized as a stable area that is slightly interrupted in Michoacán-Colima and in the northern coast of Jalisco, near the region where the major genetic divergence was located for this species (Fig. 5e). In addition, the high genetic diversity zones in Jalisco and Guerrero (Fig. 5h) are coincident with some climatic stable areas. For *M. mexicanus* the climatic stable areas were broad (Fig. 5c) and disrupted at the Guerrero–Oaxaca border, matching the

major phylogeographic division of this species (Fig. 2f). However, in this case at least one of the algorithms predicted a broad stable area spanning this phylogeographic-break area.

4. Discussion

The northern Neotropical dry forest: a spring of evolutionary lineages

Our results show that three unrelated bird species, displaying different natural histories but inhabiting the same areas in the northern Neotropical dry forest, present marked phylogeographic structure. Such structures were found within a relatively small area (<200,000 km^2) in bird species occupying apparently continuous ranges and possessing the ability for dispersal by flight. This pattern suggests an association between species diversification and the paleoecological history of the region. Although population genetic structure in birds has been documented for smaller areas, such a result is most common for organisms with low vagility (Joseph et al., 1995; Kisel and Barraclough, 2010; Milá et al., 2010). Several studies have found phylogeographic structure of mainland Neotropical bird species in broader regions (García-Moreno et al., 2004; Cadena et al., 2007; Nyári, 2007; Miller et al., 2008; Navarro-Sigüenza et al., 2008; Caparroz et al., 2009; Weir, 2009; Arbeláez-Cortés et al., 2010; Barrera-Guzmán et al., 2012), yet these and other studies have related the phylogeographic structure of Neotropical birds to the presence of geographic barriers or range changes owing to past climatic fluctuations (Cabanne et al., 2008; Burney and Brumfield, 2009; Milá et al., 2009; D'Horta et al., 2011; Naka et al., 2012).

Here, we present a new pattern for Neotropical birds, consisting of phylogeographic structure within a relatively small area without any evidence of current barriers to dispersal, which is also supported by results of other birds endemic to the region (Arbeláez-Cortés and Navarro-Sigüenza, 2013, EAC unpublished data). Our results highlight a unique situation when compared to patterns of shared phylogeographic breaks among widespread Neotropical bird species with ranges divided by geographic barriers (Burney and Brumfield, 2009; Weir, 2009; Barber and Klicka, 2010; Naka et al., 2012) as well as to the pattern of low intraspecific genetic divergence in species with continuous ranges (Bates et al., 2003). However, our results are similar to the ones of other narrowly distributed coastal lowland tropical communities of vertebrates from the Atlantic forest in Brazil, the wet tropical rainforest of northeastern Australia (Joseph et al., 1995; Schneider et al., 1998; Carnaval et al., 2009; Moussalli et al., 2009; Martins, 2011), and trees of Central America (Poelchau and Hamrick, 2013).

Based on the idea that species with overlapping ranges also share common histories, comparative phylogeography aims to detect concordant patterns among co-distributed species (Avise, 2000; Zink, 2002; Lapointe and Rissler, 2005; Carstens and Richards, 2007; Arbeláez-Cortés, 2012). Therefore, finding concordant phylogeographic structures could indicate that the same historical processes have similarly influenced all the species in one region. However, complete concordance is elusive because all species harbour intrinsic characteristics that elicit different responses to particular events, rendering idiosyncratic histories that result in different phylogeographic patterns (Schneider et al., 1998; Zink, 2002; Arbeláez-Cortés, 2012). We recognize that there are several methods to search for concordance among phylogeographic patterns of different species, (see Arbeláez-Cortés, 2012 and references therein), but here we selected CADM to explore this possibility of concordance because this method is based on genetic distances and does not require a well-resolved phylogeny. However, we did not find quantitative evidence of concordance among the two species compared. Therefore, the concordance among the phylogeographic patterns among the species is qualitative, but implies a scenario in which past environmental processes may have produced population isolation in both species.

The phylogeographic breaks found here seem to be consistent with other biogeographic patterns found in the region (Fig. 1). For example, the phylogeographic break at the Guerrero–Oaxaca border, generally shared by all three bird species, also seems to be present in at least a plant (*Spondias purpurea*, Miller and Schaal, 2005), an ant (*Azteca pittieri*, Pringle et al., 2012), a frog (*Rana forrieri*, Zaldívar-Riverón et al., 2004), a snake (*Trimorphodon biscutatus*, Devitt, 2006), and an iguana (*Ctenosaura pectinata*, Zarza et al., 2008). Besides, the division placed in Michoacán–Guerrero for *M. chrysogenys* and for *M. mexicanus*, has been also observed for two sister species of snakes (*Leptodeira* spp., Daza et al., 2009) and is near a zone of high diversification of *Bursera* trees (Becerra, 2005; Becerra and Venable, 2008). However, we also found contrasting phylogeographic patterns in the region. For example, *Campylorhynchus rufinucha* presents its major break between Oaxaca and Chiapas (Vázquez-Miranda et al., 2009), while another bird (*Icterus pustulatus*, Cortés-Rodríguez et al., 2008) and two bats (*Musonycteris harrisoni* and *Pteronotus davyi*; (Ortega et al., 2009; Guevara-Chumacero et al., 2010) did not show clear phylogeographic structure there. Another phylogeographic break in Nayarit–Jalisco, has been observed in other animals (Demastes et al., 2002; Zaldívar-Riverón et al., 2004; Mateos, 2005; Devitt, 2006; Mulcahy, 2008; Zarza et al., 2008; Pringle et al., 2012; EAC unpublished data) but here the individuals of *M. chrysogenys* and *M. mexicanus* across this zone correspond to the same haplogroup.

We also found that the ranges of the haplogroups partially match the ranges of the subspecies. The subspecies of *M. mexicanus* join their ranges in Oaxaca closer to their major phylogeographic break; while subspecies of *M. chrysogenys* have ranges that meet in Jalisco, where we found mtDNA haplogroups mixing. At a higher taxonomic level, some sister bird species share range boundaries in areas identified here as phylogeographic breaks. Such is the case of contact zones of *Ortalis poliocephala–O. leucogastra* between Guerrero and Oaxaca (e.g., Howell and Webb, 1995) and the snakes of the genera *Porthidium* and *Leptodeira* (Bryson et al., 2008; Daza et al., 2009) between Jalisco and Michoacan.

Moreover, biogeographic patterns of birds indicate that western Mexico includes three areas of endemism that roughly resemble the ranges of the haplogroups defined here, and three zones of high species turnover that are at or near the phylogeographic breaks (García-Trejo and Navarro, 2004). Therefore, such concordance among different tiers of biodiversity (i.e., aspects III and IV of genealogical concordance sensu Avise, 2000) supports a scenario of different events acting over time in roughly the same areas and leaving their imprint on the geographic patterns of the northern Neotropical dry forest biota.

Contrast between mtDNA and nDNA patterns of variation

Although we found some concordance among mtDNA and nDNA information (e.g., *P. leclancherii* CADM) these markers exhibited different levels of resolution. However, we did not found any evidence of genetic structure when the allele frequencies of all nDNA loci were analyzed. Although the most parsimonious explanation for the lower variability and associated structure found in nDNA than in mtDNA markers is the smaller effective population size and higher mutation rate of the latter, other factors, such as sex biased dispersal, cannot be ruled out (Hare, 2001; Zhang and Hewitt, 2003). Besides, in the case of the Structure analysis (Pritchard et al., 2000), the accuracy of the assignments depends on the number of individuals, number of loci, and the extent of allele-frequency differences among populations, which were low

in our analysis; and the amount of admixture, that seems to be high for some alleles in our species.

Because nDNA is bi-parentally inherited, male-biased gene flow could erode the signature of a matrilineal partition in the mtDNA. For *P. leclancherii* we found a stronger correlation between the mtDNA and the geographic and resistance distances, than between the nDNA 20454 locus and such distances. The same occurred for *M. chrysogenys* but in this species the correlation was not significant. Patterns like this have been explained for Neotropical vertebrates by differences in the range of movements between males and females (e.g., Tchaicka et al., 2007; Turmelle et al., 2011). In our case we have no evidence indicating stronger female than male philopatry in either species. However, *M. mexicanus* (which we did not analyze because of low sample size) is a sedentary species that uses the same territories to breed and forage during successive years, and there is evidence of RAPD genetic divergences over short distances (Reyes et al., 2009; Murphy et al., 2010). Because RAPD markers are largely nuclear, such differentiation could be related to philopatry of both sexes in a small spatial scale. With the data at hand we cannot conduct a detailed analysis of an ecological process like the patterns of dispersal among males and females. On other hand, the fixed allele in the GAPDH of *M. mexicanus* remains intriguing, because this locus was variable in the other species and

M. mexicanus showed deep mtDNA differentiation. More variable nDNA markers will be necessary to further understand multi-scale patterns of phylogeographic structure. However, the results of the CADM suggest that the effect of the present geographic and resistance distances on the genetic structure of two species is low and that both distances are strongly correlated, indicating that at present the environmental differences in the study area depend on the geographic distances among sites and there is not a clear environmental barrier dividing the zone. This drives us to consider the role of past historical processes (not conspicuous at present) as plausible explanations of the phylogeographic structure observed.

Insights into the history of western Mexico's biota

Geological events and climatic fluctuations during the last 20 million years have been involved in the history of western Mexico biota (Hubbard, 1973; Becerra, 2003; Zaldívar-Riverón et al., 2004; Becerra, 2005; Mateos, 2005; Devitt et al., 2008; Mulcahy, 2008; Daza et al., 2009; Ferrusquía-Villafranca et al., 2010; De-Nova et al., 2012). When we contrasted the phylogeo- graphic breaks of the three target species with a digital elevation model of the area, we can see that they coincide with areas where elevations above 1900 m are close to the coast (<26 km) such as the Sierra de Coalcomán in Michoacán, and the Sierra Madre del Sur (SMS) in Guerrero. Such a coarse concordance among phyloge- ographic breaks in lowland species, and the proximity of mountains suggests a role of geological events in shaping phylogeographic pat- terns. In fact, the radiation of Bursera trees and the speciation of some fishes and snakes in the region seem to be associated with geological activity of the Trans Mexican Volcanic Belt (TMVB) (Mateos et al., 2002; Becerra, 2005; Mateos, 2005; Devitt et al., 2008; De-Nova et al., 2012). However, the orogenesis of western Mexico predates the divergence dates found here. The TMVB orogenesis was 20–3 million years ago (Becerra, 2005; Devitt, 2006), and the geologic activity in the SMS is even older (35–20 million years ago, Morán-Zenteno et al., 2000). However, we cannot rule out indirect effects of these mountains, such as generating climatic instability in the lowlands, which could have narrowed the width of the coastal plains and caused a reduction in gene flow.

Phylogeographic analysis and climatically stable areas suggest that the climatic oscillations are a plausible leading process to explain the patterns observed. We consider a scenario in which temperature fluctuations generated changes in species ranges promoting the evolution of different lineages from isolated populations. This scenario is supported by the following evidence: (1) the tropical dry forest of western Mexico is dominated by Bursera, a plant that does not tolerate temperatures below 0 °C (Becerra, 2005; De-Nova et al., 2012); (2) Potential vegetation maps of the Mexican Pleistocene indicate that the tropical dry forest was fragmented by tracts of coniferous and tropical rain forests (Ceballos et al., 2010); (3) An 8 °C decrease documented for TMVB during the last 25,000 years (Caballero et al., 2010) could have changed the climate in adjacent Mexico lowlands, (4) Paleoecological data from the last 9600 years indicate that the Neotropical dry forest has been replaced by moister forests or open savannah-like vegetation (Piperno and Jones, 2003; Berrio et al., 2006; González-Carranza et al., 2008); and (5) sediment core information for the last 2700 years in the Balsas Basin, indicates that in a 1000-year period, the tropical dry forests decreased, while mesophylic forest increased and dominated, then the dry forest expanded again (Berrio et al., 2006). Although the last evidence is from recent periods that do not match the time frame of the patterns observed, all of them point clearly to a history of periodic change and fragmentation of the tropical dry forests where the species are found today.

In *M. chrysogenys* and *P. leclancherii*, haplogroup diversification was estimated to have taken place during the last 122,000 years. We found one of the climatic stable zones of *P. leclancherii* and *M. chrysogenys* in eastern Oaxaca, coinciding with an area of endemism and diversification of Bursera (Espinosa et al., 2006; Becerra and Venable, 2008), and near a putative refuge in the Isthmus of Tehuantepec (Hubbard, 1973) that was also detected by phylogeographic data of one bat (Guevara-Chumacero et al., 2010). Additionally, the higher genetic diversity of *P. leclancherii* in this area is consistent with a refuge scenario. Isolated populations of *P. leclancherii* could have persisted along the Guerrero coast and for *M. chrysogenys* isolated populations could have also persisted more to the north (Jalisco–Nayarit), where analyses indicate the presence of climatically stable areas and high genetic diversity. Indeed, as expected under a climatic refuge scenario, we found evidence of demographic growth for almost all of the species haplogroups, a trend documented for other vertebrates in the region (Cortés-Rodríguez et al., 2008; Zarza et al., 2008; Vázquez-Miranda et al., 2009; Guevara-Chumacero et al., 2010). For *M. mexicanus*, we found the more widespread climatically stable areas, suggesting the existence of an almost continuous range during their recent history, and an older date of haplogroup differentiation. However, the areas where the haplogroups of *M. mexicanus* evolved could be near the ones identified for the other two species. Therefore, our results raise the possibility that two zones (the Guerrero–Oaxaca border and the area between southern Jalisco and Michoacán) have been promoting diversification in the northern Neotropical dry forest for a long time.

5. Conclusions

The phylogeographic patterns of the three bird species studied, their Environmental Niche Models projections, and evidence from other studies, point to a scenario of population isolation that occurred in the northernmost range of the Neotropical dry forest. This scenario suggests that the tropical dry forest of western Mexico was fragmented during the last million years owing to climatic fluctuations and leading to the occurrence of similar vicariant events. Larger datasets will help refine the definition of the areas where the phylogeographic breaks occur, but the main result showing that the three species have phylogeographic breaks in roughly the same areas is unlikely to change substantially with additional data. Our results raise a question about the kind of sharp ecological changes that occurred in the region and that drove

population divergence, even in species with high tolerance for anthropogenic habitat disturbance and high dispersal capacity. The tropical dry forest of western Mexico is a hotspot of endemism, home to numerous taxa with diverse histories, and it is thus an important area in which to study the recent lineage diversification of Neotropical biotas.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.10.006.

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Additional file 1 Table S1 List of samples, locality information, and sequences included in this work. GenBank accession number is indicated .

Taxon	Collection Number	State	Locality	latitude	longitude	ND2	COI	Cyt B	20454 Locus	GAPD	TGFB	MUSK
Passerina leclancherii	DNL S/N (1472)	OAXACA	Santa Cruz Huatulco	15.7666667	-96.1333333	KF752719	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Passerina leclancherii	JK04-240	OAXACA	Puerto Escondido a 5 Km N	15.9252778	-97.1672222	KF752720	n.a.	KF752784	KF752843	KF753160	KF752913	KF753193
Passerina leclancherii	CHIS 166	CHIAPAS	Laguna la Joya, 7 km rancho vergel, Mpio. Tonala	15.9645	-93.7024	KF752721	n.a.	KF752785	KF752844	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 454	OAXACA	Manaltepec, Río	16.1147222	-97.2961111	KF752722	n.a.	KF752786	KF752845	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 404	OAXACA	Manaltepec, Río	16.1147222	-97.2961111	KF752723	n.a.	KF752787	KF752846	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 406	OAXACA	Manaltepec, Río	16.1147222	-97.2961111	KF752724	n.a.	KF752788	KF752847	KF753161	KF752914	KF753194
Passerina leclancherii	CHIS 455	OAXACA	Manaltepec, Río	16.1147222	-97.2961111	KF752725	n.a.	n.a.	KF752848	n.a	n.a.	n.a.
Passerina leclancherii	CHIS 407	OAXACA	Manaltepec, Río	16.1147222	-97.2961111	n.a.	n.a.	n.a.	KF752849	n.a	n.a.	n.a.
Passerina leclancherii	UWBM (cwt034)	CHIAPAS	Arriaga	16.2694	-93.8644	EF529887	n.a.	n.a.	n.a.	n.a	n.a.	n.a.
Passerina leclancherii	CHIS 170	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF752726	n.a.	KF752789	KF752850	KF753162	KF752915	KF753195
Passerina leclancherii	CHIS 185	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF752783	n.a.	KF752790	KF752851	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 179	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF752727	n.a.	KF752791	KF752852	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 187	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF752728	n.a.	KF752792	KF752853	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 199	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	n.a.	n.a.	n.a.	KF752854	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 171	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	n.a.	n.a.	n.a.	KF752855	n.a.	n.a.	n.a.
Passerina leclancherii	CHIS 200	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	n.a.	n.a.	n.a.	KF752856	n.a.	n.a.	n.a.

Passerina leclancherii	CHIS 175	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF752729	n.a.	KF752793	n.a.	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 050	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752776	n.a.	KF752794	KF752857	KF753163	KF752916	KF753196
Passerina leclancherii	CONACY T04 029	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752730	n.a.	KF752795	KF752858	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 057	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752731	n.a.	KF752796	KF752859	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 078	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752732	n.a.	KF752797	KF752860	KF753164	KF752917	KF753197
Passerina leclancherii	CONACY T04 097	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752777	n.a.	KF752798	KF752861	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 107	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752778	n.a.	KF752799	KF752862	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 147	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752733	n.a.	KF752800	KF752863	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 054	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752779	n.a.	KF752801	KF752864	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T04 113	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF752734	n.a.	KF752802	KF752865	n.a.	n.a.	n.a.
Passerina leclancherii	OMVP 0774	OAXACA	Cerro Piedra Larga	16.6066667	-95.8	KF752735	n.a.	KF752803	KF752866	KF753165	KF752918	KF753198
Passerina leclancherii	OMVP 0746	OAXACA	Cerro Piedra Larga	16.6066667	-95.8	KF752736	n.a.	KF752804	KF752867	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T 1476	OAXACA	Nizanda, Camino al Aguaje	16.632563	-94.990109	KF752737	n.a.	KF752805	KF752868	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T 1459	OAXACA	Nizanda, Agua Tibia	16.65	-95.017	KF752738	n.a.	KF752806	KF752869	KF753166	KF752919	KF753199
Passerina leclancherii	CONACY T 1468	OAXACA	Nizanda, Agua Tibia	16.65	-95.017	KF752739	n.a.	KF752807	KF752870	n.a.	n.a.	n.a.
Passerina leclancherii	CONACY T 1315	OAXACA	Nizanda, El Aguaje	16.6883	-95.1266	KF752740	n.a.	KF752808	KF752871	n.a.	n.a.	n.a.
Passerina leclancherii	ORT11-93	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71862	-99.62672	KF752741	n.a.	KF752809	KF752872	n.a.	n.a.	n.a.
Passerina leclancherii	ORT11-91	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71951	-99.62067	KF752742	n.a.	KF752810	KF752873	n.a.	n.a.	n.a.
Passerina leclancherii	ORT11-94	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71951	-99.62067	KF752743	n.a.	KF752811	KF752874	n.a.	n.a.	n.a.

Passerina leclancherii	ORT11-60	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71951	-99.62067	KF752744	n.a.	KF752812	KF752875	n.a.	KF752920	KF753200
Passerina leclancherii	CONACYT 1579 (NIZA06)	OAXACA	Nizanda, Piedra Azul	16.7452777	-95.115	KF752745	n.a.	KF752813	KF752876	n.a.	n.a.	n.a.
Passerina leclancherii	HJ6-030	GUERRERO	Laguna Coyuca, Vicente Guerrero, Cerca a Coyuca, en selva mediana	17.05206	-100.32311	KF752746	n.a.	n.a.	KF752877	KF753167	KF752921	KF753201
Passerina leclancherii	CONACYT 905	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752780	n.a.	KF752814	KF752878	KF753168	KF752922	KF753202
Passerina leclancherii	PFA 027 (15581)	GUERRERO	Cañón del Zopilote	17.7763889	-99.575	n.a.	n.a.	n.a.	KF752879	n.a.	n.a.	n.a.
Passerina leclancherii	JK04-223	GUERRERO	Carrizal de Bravo	17.816713	-99.967595	KF752747	n.a.	KF752815	KF752880	n.a.	n.a.	n.a.
Passerina leclancherii	JK04-220	GUERRERO	Carrizal de Bravo	17.816713	-99.967595	KF752748	n.a.	KF752816	KF752881	KF753169	KF752923	KF753203
Passerina leclancherii	JK04-221	GUERRERO	Carrizal de Bravo	17.816713	-99.967595	KF752749	n.a.	KF752817	KF752882	n.a.	n.a.	n.a.
Passerina leclancherii	MZFC04 255	GUERRERO	San Miguel Tecuiciapan Mpio Tepecuhcuilcon de Trujanio	17.961	-99.3990278	KF752750	n.a.	n.a.	KF752883	n.a.	n.a.	
Passerina leclancherii	BAL 261	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752751	n.a.	KF752818	KF752884	KF753170	KF752924	KF753204
Passerina leclancherii	BAL 289	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752781	n.a.	KF752819	KF752885	n.a.	n.a.	
Passerina leclancherii	BAL 314	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752752	n.a.	KF752820	KF752886	KF753171	KF752925	KF753205
Passerina leclancherii	AZAR 06	GUERRERO	Campo Morado, Mpio Arcelia	18.1917222	-100.162083	KF752753	n.a.	KF752821	KF752887	KF753172	KF752926	KF753206
Passerina leclancherii	CONACYT 1041	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752754	n.a.	KF752822	KF752888	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 1027	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752755	n.a.	KF752823	KF752889	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 1028	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752756	n.a.	KF752824	KF752890	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 1035	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752757	n.a.	KF752825	KF752891	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 1036	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752758	n.a.	KF752826	KF752892	KF753173	KF752927	KF753207

Passerina leclancherii	CONACYT 1038	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752759	n.a.	KF752827	KF752893	KF753174	KF752928	KF753208
Passerina leclancherii	CONACYT 1031	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752760	n.a.	KF752828	n.a.	n.a.	n.a.	n.a.
Passerina leclancherii	PFA 004	GUERRERO	Las Tinajas	18.355	-100.723333	n.a.	n.a.	n.a.	KF752894	n.a.	n.a.	n.a.
Passerina leclancherii	HUAU-25	MORELOS	Jojutla, 16 Km SE CercaPueblo Huautla	18.4355667	-99.0014667	KF752761	n.a.	KF752829	KF752912	n.a.	n.a.	n.a.
Passerina leclancherii	HUAU-01	MORELOS	Jojutla, Huautla, 25.75 km SE.	18.4369722	-99.0024444	KF752775	n.a.	KF752830	KF752895	KF753175	KF752929	KF753209
Passerina leclancherii	HUAU-04	MORELOS	Jojutla, Huautla, 25.75 km SE.	18.4369722	-99.0024444	KF752762	n.a.	KF752831	KF752896	n.a.	n.a.	n.a.
Passerina leclancherii	JCD S/N (2483)	ESTADO DE MEXICO	Bejucos	18.775	-100.425	KF752763	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 862	COLIMA	Las Cuevas	18.9516944	-103.509111	n.a.	n.a.	n.a.	KF752897	n.a.	n.a.	n.a.
Passerina leclancherii	CONACYT 850	COLIMA	Las Cuevas	18.9516944	-103.509111	KF752764	n.a.	KF752832	KF752898	KF753176	KF752930	KF753210
Passerina leclancherii	CONACYT 853	COLIMA	Las Cuevas	18.9516944	-103.509111	KF752765	n.a.	KF752833	KF752899	n.a.	n.a.	KF753211
Passerina leclancherii	Cham10-07	JALISCO	Estacion Biologica Chamela	19.5	-105.04	KF752766	n.a.	KF752834	KF752900	n.a.	n.a.	n.a.
Passerina leclancherii	GRK037	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752767	n.a.	KF752835	KF752901	n.a.	n.a.	n.a.
Passerina leclancherii	MZFC23295 (GRK032)	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752768	n.a.	KF752836	KF752902	n.a.	n.a.	n.a.
Passerina leclancherii	MZFC23302 (GRK010)	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752769	n.a.	KF752837	KF752903	KF753177	KF752931	KF753212
Passerina leclancherii	MZFC23304 (GRK003)	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752770	n.a.	KF752838	KF752904	n.a.	n.a.	n.a.
Passerina leclancherii	CHAM-0710	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454167	-105.083861	KF752771	n.a.	KF752839	KF752905	n.a.	n.a.	n.a.

Passerina leclancherii	CHAM-07 13	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454167	-105.083861	KF752782	n.a.	KF752840	KF752906	n.a.	n.a.	n.a.
Passerina leclancherii	CHAM-07 14	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454167	-105.083861	n.a.	n.a.	KF752841	KF752907	n.a.	n.a.	n.a.
Passerina leclancherii	CHAM-07 12	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454167	-105.083861	n.a.	n.a.	n.a.	KF752908	n.a.	n.a.	n.a.
Passerina leclancherii	CHAM-07 11	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454167	-105.083861	KF752772	n.a.	KF752842	n.a.	n.a.	n.a.	n.a.
Passerina leclancherii	ORT11-45	JALISCO	El Manantial, Mpio Tamatlan	19.8294722	-105.235333	KF752773	n.a.	n.a.	KF752909	KF753178	KF752932	KF753213
Passerina leclancherii	ORT11-46	JALISCO	El Manantial, Mpio Tamatlan	19.8294722	-105.235333	n.a.	n.a.	n.a.	KF752910	n.a.	n.a.	n.a.
Passerina leclancherii	ORT11-50	JALISCO	El Manantial, Mpio Tamatlan	19.8294722	-105.235333	KF752774	n.a.	n.a.	KF752911	n.a.	n.a.	n.a.
Passerina versicolor (outgroup)	UWBM CWT095					EF529888	n.a.	AF301457.1	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	JK04-231	OAXACA	Puerto Escondido a 5 Km N	15.9252778	-97.1672222	KF752933	KF752986	n.a.	KF753032	KF753179	KF753070	KF753214
Melanerpes chrysogenys	AV 838	GUERRERO	El coco	18.0666	-100.475	KF752979	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-036	GUERRERO	Cerca a Laguna de Tres Palos	16.70173	-99.63757	KF752934	KF752987	n.a.	KF753033	n.a	KF753071	KF753215
Melanerpes chrysogenys	ORT11-110	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.72149	-99.51575	KF752935	n.a.	n.a.	n.a	n.a	n.a.	n.a.
Melanerpes chrysogenys	ORT11-75	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.72186	-99.61961	KF752936	KF752988	n.a.	n.a.	n.a	n.a.	n.a.
Melanerpes chrysogenys	ORT11-97	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.72186	-99.61961	KF752937	KF752989	n.a.	n.a.	n.a	n.a.	n.a.
Melanerpes chrysogenys	ORT11-98	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.72186	-99.61961	KF752938	KF752990	n.a.	n.a.	n.a	n.a.	n.a.
Melanerpes chrysogenys	NAY 034	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.72227	-99.61967	KF752939	KF752991	n.a.	KF753034	n.a	n.a.	n.a.

Melanerpes chrysogenys	HJ6-056	GUERRERO	Entre Lomas de Chapultepec y La estacion, cerca a Rio Chacalapa	16.72318	-99.60116	KF752940	KF752992	n.a.	KF753035	n.a	n.a.	n.a.
Melanerpes chrysogenys	HJ6-058	GUERRERO	Entre Lomas de Chapultepec y La estacion, cerca a Rio Chacalapa	16.72318	-99.60116	KF752941	KF752993	n.a.	KF753036	KF753180	KF753072	KF753216
Melanerpes chrysogenys	TECO08-17	GUERRERO	Tecomate pesqueria	16.7426389	-99.3632222	KF752942	KF752994	n.a.	KF753037	KF753181	KF753073	KF753217
Melanerpes chrysogenys	TECO08-09	GUERRERO	Tecomate pesqueria	16.7426389	-99.3632222	KF752943	KF752995	n.a.	KF753038	KF753182	KF753074	KF753218
Melanerpes chrysogenys	CHIS 478	GUERRERO	Tecomate	16.8044444	-99.4552778	KF752944	KF752996	n.a.	KF753039	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CHIS 486	GUERRERO	Tecomate	16.8044444	-99.4552778	KF752945	KF752997	n.a.	KF753040	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-028	GUERRERO	Laguna Mitla, entre laguna y mar	17.01468	-100.27547	KF752946	KF752998	n.a.	KF753041	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-029	GUERRERO	Laguna Coyuca, Vicente Guerrero, Cerca a Coyuca	17.05206	-100.32311	KF752947	KF752999	n.a.	KF753042	KF753183	KF753075	KF753219
Melanerpes chrysogenys	HJ6-024	GUERRERO	Rodesia, Mpio Tecpan, cerca Laguna el Plan	17.19592	-100.71378	KF752980	n.a.	n.a.	KF753043	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-019	GUERRERO	Laguna Nuxco, Tecpan, Selva baja	17.19606	-100.80467	KF752948	KF753000	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-021	GUERRERO	Laguna Nuxco, Tecpan, Selva baja	17.19606	-100.80467	KF752949	KF753001	n.a.	KF753044	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HJ6-020	GUERRERO	Laguna Nuxco, Tecpan, Selva baja	17.19606	-100.80467	KF752950	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 889	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752981	KF753002	n.a.	KF753045	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 908	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752951	KF753003	n.a.	KF753046	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 895	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752952	KF753004	n.a.	KF753047	n.a.	KF753076	KF753220
Melanerpes chrysogenys	CONACY T 916	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752953	KF753005	n.a.	KF753048	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 926	GUERRERO	Frac. Laguna Nuxco	17.2033333	-100.796667	KF752954	KF753006	n.a.	KF753049	n.a.	n.a.	n.a.

Melanerpes chrysogenys	HJ6-011	GUERRERO	Barra de San Valentin, Playa entre mar y laguna	17.48221	-101.33173	KF752955	KF753007	n.a.	KF753050	KF753184	KF753077	KF753221
Melanerpes chrysogenys	HJ6-012	GUERRERO	Barra de San Valentin, Playa entre mar y laguna	17.48221	-101.33173	KF752956	KF753008	n.a.	KF753051	n.a.	n.a.	n.a.
Melanerpes chrysogenys	BAL 307	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752957	KF753009	n.a.	KF753052	n.a.	n.a.	n.a.
Melanerpes chrysogenys	BAL 318	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752958	KF753010	n.a.	KF753053	n.a.	n.a.	n.a.
Melanerpes chrysogenys	BAL 276	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752959	KF753011	n.a.	KF753054	KF753185	n.a.	KF753222
Melanerpes chrysogenys	BAL 306	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF752960	KF753012	n.a.	KF753055	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 1085	MICHOACAN	Presa Infiernillo, 1km N Campamento CFE	18.2716667	-101.891667	KF752961	KF753013	n.a.	KF753056	KF753186	KF753078	KF753223
Melanerpes chrysogenys	TXP 03	GUERRERO	Cerro Tuxpan	18.3581194	-99.4757278	KF752962	KF753014	n.a.	KF753057	KF753187	KF753078	KF753224
Melanerpes chrysogenys	TXP 09	GUERRERO	Cerro Tuxpan	18.3581194	-99.4757278	KF752978	KF753015	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	AG 053	GUERRERO	3 km S Las Juntas de Cujarán, 13 km W Aratichanguio	18.425	-101.448333	KF752963	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HUAU 02	MORELOS	Jojutla, Huautla 25.75 km SE.	18.4369722	-99.0024444	KF752982	KF753016	n.a.	KF753058	n.a.	KF753080	n.a.
Melanerpes chrysogenys	HUAU 06	MORELOS	Jojutla, Huautla 25.75 km SE.	18.4369722	-99.0024444	KF752983	KF753017	n.a.	KF753059	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HUAU 03	MORELOS	Jojutla, Huautla 25.75 km SE.	18.4369722	-99.0024444	KF752964	KF753018	n.a.	KF753060	n.a.	n.a.	n.a.
Melanerpes chrysogenys	HUAU 08	MORELOS	Jojutla, Huautla 25.75 km SE.	18.4369722	-99.0024444	KF752965	KF753019	n.a.	KF753061	n.a.	n.a.	n.a.
Melanerpes chrysogenys	CONACY T 847	COLIMA	Las Cuevas	18.9516944	-103.509111	KF752966	KF753020	n.a.	KF753062	KF753188	KF753081	KF753225
Melanerpes chrysogenys	Cham10-02	JALISCO	Borde Rio Chamela, Mpio La Huerta	19.52672	-105.06924	KF752967	KF753021	n.a.	n.a.	n.a	KF753082	KF753226
Melanerpes chrysogenys	CHAM08-18	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752968	KF753022	n.a.	KF753063	n.a.	n.a.	n.a.

Melanerpes chrysogenys	CHAM08-19	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752969	KF753023	n.a.	KF753064	n.a.	n.a.	n.a.
Melanerpes chrysogenys	MZFC23326 (GRK 017)	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.5454166	-105.083861	KF752970	KF753024	n.a.	KF753065	n.a.	KF753083	KF753227
Melanerpes chrysogenys	Cham10-03	JALISCO	La Huerta, Club vacacional chamela seccion 47	19.54565	-105.08138	KF752971	KF753025	n.a.	KF753066	KF753189	KF753084	KF753228
Melanerpes chrysogenys	URRA71	JALISCO	El Pochote, Mpio. Toliman	19.59591	-103.94241	KF752984	n.a.	n.a.	n.a.	KF753192	n.a.	n.a.
Melanerpes chrysogenys	URRA08	JALISCO	Rancho Primavera, El Tuito, Mpio. Cabo Corrientes	20.34523	-105.3575	KF752985	KF753031	n.a.	KF753069	n.a.	n.a.	n.a.
Melanerpes chrysogenys	ORT11-32	JALISCO	Mpio. Pto Vallarta	20.6744444	-104.961944	KF752972	KF753026	n.a.	n.a.	KF753190	KF753085	KF753229
Melanerpes chrysogenys	ORT 055	NAYARIT	Mpio Bahia Balderas 3KM N Fortuna de Vallejo	20.9608	-105.1336	KF752973	KF753027	n.a.	KF753067	n.a	KF753086	KF753230
Melanerpes chrysogenys	FRG 543	NAYARIT	Mecatán, 15 km NW Jalcocotán	21.5383333	-105.108333	KF752974	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Melanerpes chrysogenys	ORT 004	NAYARIT	3.5Km N de Syngaita, Mpio San Blas	21.6031	-105.2377	KF752975	KF753028	n.a.	n.a.	n.a.	n.a.	KF753231
Melanerpes chrysogenys	MFOR 150	SINALOA	El salto, aprox 20 Km al NW de Mazatlan	23.3625	-105.694833	KF752976	KF753029	n.a.	KF753068	n.a.	KF753087	KF753232
Melanerpes chrysogenys	SAR 7937	SINALOA	Mazatlan 20 Km NW, near el Salto	23.3625	-106.305167	KF752977	KF753030	n.a.	n.a.	KF753191	n.a.	KF753233
Melanerpes carolinus (Outgroup)	USNM 626309 / LPBO1162-92503					DQ361284.1	DQ434640.1	n.a.	n.a.	n.a.	n.a.	n.a.
Momotus mexicanus	Chis 360	Chiapas	Rancho La Industria	16.1580556	-93.8066667	KF753088	KF753116	n.a.	KF753139	KC556752	n.a.	n.a.
Momotus mexicanus	CHIS 375	CHIAPAS	Rancho La Industria	16.1580556	-93.8066667	KF753089	KF753117	n.a.	n.a.	KC556753	n.a.	n.a.
Momotus mexicanus	CHIS 374	CHIAPAS	Rancho La Industria	16.1580556	-93.8066667	n.a.	n.a.	n.a.	KF753140	KC556754	n.a.	n.a.
Momotus mexicanus	CHIS 174	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF753090	KF753118	n.a.	n.a.	KC556755	n.a.	n.a.
Momotus mexicanus	CHIS 169	CHIAPAS	Ejido Adolfo López Mateos	16.303057	-93.874628	KF753091	KF753119	n.a.	n.a.	n.a.	n.a.	n.a.

Momotus mexicanus	CONACY T04 019	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF753092	KF753120	n.a.	KF753141	KC556756	n.a.	n.a.
Momotus mexicanus	CONACY T04 155	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	KF753093	KF753121	n.a.	KF753142	KC556757	n.a.	n.a.
Momotus mexicanus	CONACY T04 020	OAXACA	Santa María Lachixonace	16.44958	-95.8296382	n.a.	KF753122	n.a.	n.a.	n.a.	n.a.	n.a.
Momotus mexicanus	CHIS 392	OAXACA	Rancho Las Minas	16.5147222	-94.2183333	KF753094	KF753123	n.a.	KF753143	KC556758	n.a.	n.a.
Momotus mexicanus	NAY 016	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71776	-99.62125	KF753095	KF753124	n.a.	KF753144	KC556759	n.a.	n.a.
Momotus mexicanus	ORT11-73	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71776	-99.62125	KF753096	KF753125	n.a.	KF753145	KC556760	n.a.	n.a.
Momotus mexicanus	ORT11-81	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71776	-99.62125	KF753097	KF753126	n.a.	KF753146	KC556761	n.a.	n.a.
Momotus mexicanus	ORT11-85	GUERRERO	1km N. Ejido Lomas de Chapultepec, Acapulco	16.71776	-99.62125	KF753098	KF753127	n.a.	KF753147	KC556762	n.a.	n.a.
Momotus mexicanus	HJ6-042	GUERRERO	Entre Lomas de Chapultepec y La estacion, cerca a Rio Chacalapa	16.72318	-99.60116	KF753099	KF753128	n.a.	KF753148	KC556763	n.a.	n.a.
Momotus mexicanus	TECO08-10	GUERRERO	Tecomate pesqueria	16.7426389	-99.3632222	KF753100	KF753129	n.a.	KF753149	KC556764	n.a.	n.a.
Momotus mexicanus	OMVP 0674	OAXACA	Yucunino, cerca de Santa Ana del Progreso, Putla	16.8283333	-97.88	KF753101	KF753130	n.a.	KF753150	n.a.	n.a.	n.a.
Momotus mexicanus	CONACY T 984	GUERRERO	El Carmen 2km NE	16.8361667	-98.74725	KF753102	KF753131	n.a.	KF753151	KC556765	n.a.	n.a.
Momotus mexicanus	Donado06-12	GUERRERO	Carretera cerca a Chilpancingo	17.3	-99.8	KF753113	n.a.	n.a.	KF753158	n.a	n.a.	n.a.
Momotus mexicanus	OMVP 0178	OAXACA	El Amate Putla	17.5003	-98.2642	KF753113	KF753132	n.a.	KF753152	KC556766	n.a.	n.a.
Momotus mexicanus	OMVP 0906	OAXACA	El Venado	17.5866667	-97	n.a.	KF753133	n.a.	n.a.	KC556767	n.a.	n.a.
Momotus mexicanus	BAL 315	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF753104	KF753134	n.a.	KF753153	KC556768	n.a.	n.a.
Momotus mexicanus	BAL 328	GUERRERO	San Miguel Tecuiciapan, Tlalalpa	18.0277778	-99.515	KF753105	KF753135	n.a.	KF753154	KC556769	n.a.	n.a.

Momotus mexicanus	CONACYT 1110	MICHOACAN	Cortina Presa Infiernillo	18.2716667	-101.891667	KF753106	KF753136	n.a.	n.a.	KC556770	n.a.	n.a.
Momotus Mexicanus	AV 612	GUERRERO	Zindaró el Tondoche	18.45	-100.9666	KF753107	n.a.	n.a.	n.a.	KC556771	n.a.	n.a.
Momotus mexicanus	HUAU-27	MORELOS	Jojutla, 16 Km SE CercaPueblo Huautla	18.4355667	-99.0014667	KF753108	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Momotus mexicanus	HUAU-28	MORELOS	Jojutla, 16 Km SE CercaPueblo Huautla	18.4355667	-99.0014667	KF753109	n.a.	n.a.	n.a.	KC556772	n.a.	n.a.
Momotus mexicanus	HUAU-24	MORELOS	Jojutla, 16 Km SE CercaPueblo Huautla	18.4355667	-99.0014667	KF753110	n.a.	n.a.	n.a.	KC556773	n.a.	n.a.
Momotus mexicanus	HUAU-31	MORELOS	Jojutla, 16 Km SE CercaPueblo Huautla	18.4355667	-99.0014667	n.a.	n.a.	n.a.	KF753155	KC556774	n.a.	n.a.
Momotus mexicanus	URRA73	JALISCO	El Petacal, Ejido San Isidro Potrero Grnade, Mpio Toliman	19.58274	-103.85977	KF753114	n.a.	n.a.	KF753159	n.a.	n.a.	n.a.
Momotus mexicanus	URRA74	JALISCO	El Petacal, Ejido San Isidro Potrero Grnade, Mpio Toliman	19.58274	-103.85977	KF753115	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Momotus mexicanus	ORT 034	NAYARIT	Mpio Bahia Balderas 3KM N Fortuna de Vallejo	20.9608	-105.1336	KF753111	KF753137	n.a.	KF753156	KC556775	n.a.	n.a.
Momotus mexicanus	ORT 066	NAYARIT	Mpio Bahia Balderas 3KM N Fortuna de Vallejo	20.9608	-105.1336	KF753112	KF753138	n.a.	KF753157	KC556776	n.a.	n.a.
Momotus momota (Outgroup)	JAP 174 / 528-21					JQ445580.1	EU442306.1	n.a.	n.a	n.a	n.a.	na.

SUPPORTING INFORMATION

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Additional file 2

Table S2. Internal primers designed to amplify the ND2 region of the three bird species analyzed in this study.

Primer	Sequence	Species
eac-ND2HIn1	5'GAGATDGADGAGAAGGCTA3'	*M. chrysogenys, M. mexicanus*
eac-ND2HIn2	5' GATGACCACTATTCAGCCTAA 3'	*P. leclancherii*
eac-ND2LInt1	5'CTTAACCAAACKCAAATCC 3'	*M. chrysogenys, P. leclancherii,*
eac-ND2LIn2	5' CCATAGCAATAGCATCAGCAG 3'	*M. mexicanus*

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Additional file 3

Table S3. PCR protocols used to amplify mtDNA and nDNA regions of the three bird species analyzed in this study.

DNA region	PCR protocol
ND2 and COI	10 cycles (94 °C x 15 s,55 °C x 30 s, 72 °C x 30 s) 35 cycles (94 °C x 15 s, 50 °C x 30 s, 72 °C x 30 s) 72 °C x 7 min
ND2 (internal primers)*	5 cycles (95 °C x 30 s, 57 °C, 58°C, or 59 °C x 30 s, 72 °C for 1 min), 5 cycles (95 °C x 15 s, 54 °C, 55 °C, or 57 °C x 30 s, 72 °C for 1 min) 35 cycles (94 °C x 15 s, 51 °C x 30 s, 72 °C x 30 s) 72 °C x 7 min.
CytB	27 cycles (95 °C x 1 min, 50 °C x 1 min, 72 °C x 2 min) 7 min at 72 °C
20454**	20 cycles (95 °C x 30 s, 65 to 55 °C for 1 min decreasing temperature with 1°C each two cycles, 72 °C x 1 min) 20 cycles (95 °C x 30 s, 55 °C x 30 s, 72 °C x 1 min) 72 °C x 5 min.
Gapdh	35 cycles (94 °C x 1 min, 57 °C x 45 s, 72 °C x 1 min) 72 °C x 10 min
MUSK	15 cycles (95 °C x 20 s, 58 to 54 °C x 20 s decreasing temperature with 2°C each five cycles, 72 °C x 1 min 15 s) 25 cycles (94 °C x 20 s, 52 °C x 20 s, 72 °C x 30 s) 72 °C x 10 min
TGFB	5 cycles (95 °C x 20 s, 55 °C x 20 s, 72 °C x 1 min 15 s) 5 cycles (95 °C x 20 s, 54 °C

x 20 s, 72 °C x 1 min 15 s) 35 cycles (94 °C x 20 s, 50 °C x 20 s, 72 °C x 1min 15 s)
72 °C x 10 min

*****Variation in annealing temperature are owing to the different primers used for each species

** We also used a touch-down protocol decreasing annealing temperature from 52°C to 46°C each five cycles.

SUPPORTING INFORMATION

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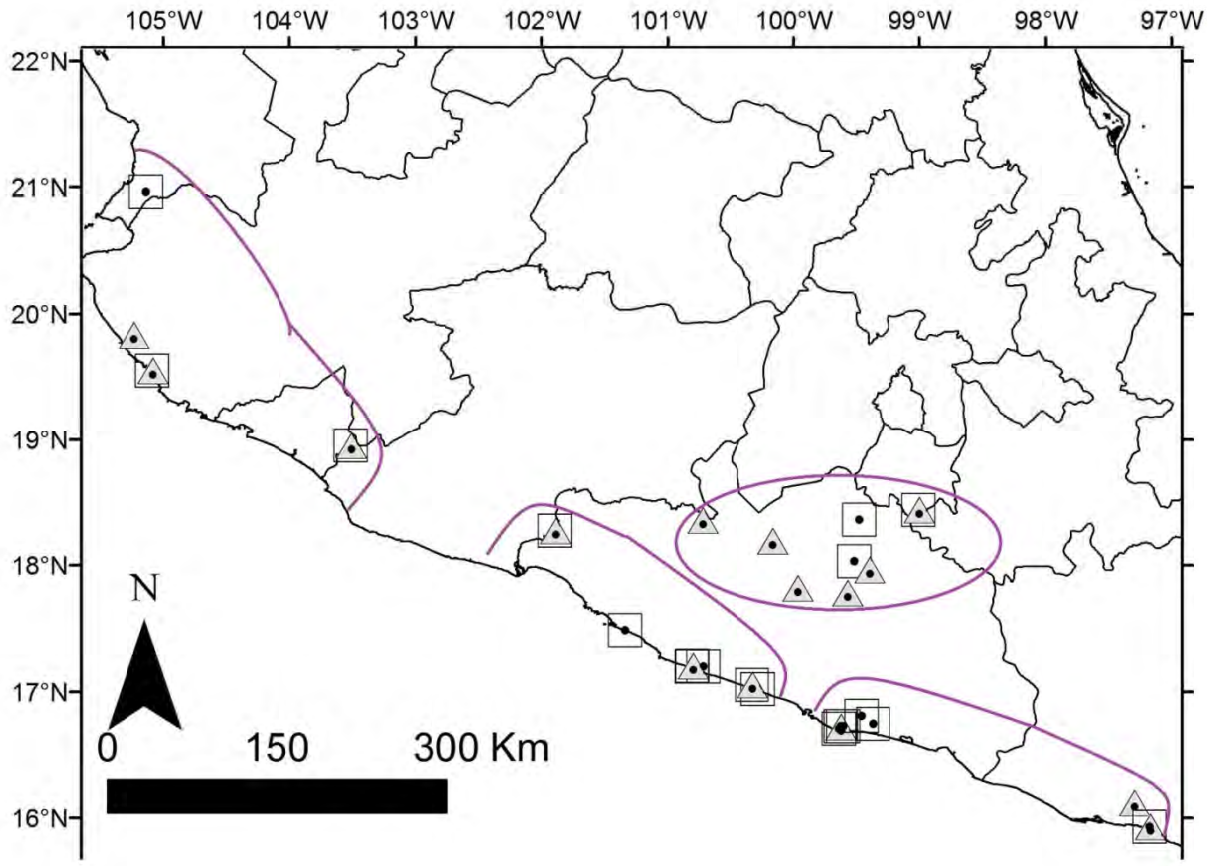
Additional file 4

Figure S1. Sample localities of two bird species from western Mexico used in the CADM analysis for the grouping (four regional groups) schema. 'Triangles' are for *P. leclancherii* and 'squares' for *M. chrysogenys*. The four regional groups are depicted (lines around the localities).



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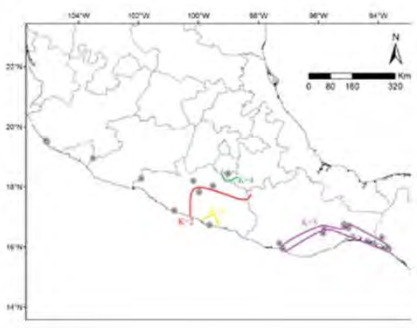
Additional file 5

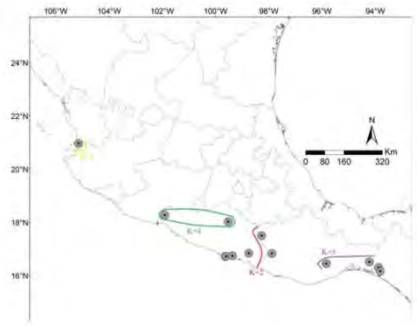
FigureS2. Location of the divergences according to SAMOVA for the mtDNA dataset of three bird species endemic to western Mexico. K values are depicted.

Passerina leclancherii



Melanerpes chrysogenys

Momotus mexicanus



SUPPORTING INFORMATION

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Additional file 6

Table S5. World clim variables used in the ENMs for each species

	P. leclancherii	*M. chrysogenys*	*M. mexicanus*
Bio2		x	x
Bio3	x	x	x
Bio4	x	x	x
Bio5	x	x	x
Bio6	x	x	x
Bio7	x	x	x
Bio8		x	x
Bio9		x	x
Bio11	x		
Bio14		x	
Bio15	x	x	x
Bio16	x	x	x
Bio17	x	x	x
Bio18	x	x	x
Bio19	x	x	x
Haspect	x	x	x
Hslope	x	x	x
Topoindex	x	x	x

CAPÍTULO 4

Consenso de la información filogeográfica de siete especies de aves endémicas: Un bosquejo de la historia reciente del oeste de México

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Introducción

La diversidad es el atributo más conspicuo de la vida en la Tierra, pero su distribución geográfica muestra un sesgo con números altos de especies (*i.e*., riqueza) en los trópicos (Orme *et al.*, 2005; Kier *et al.*, 2009). En particular para las aves, la región neotropical es la más biodiversa (Newton, 2003), pero su relevancia no se limita a una alta riqueza de especies, sino que el nivel de endemismo (*i.e*., especies de rango restringido) es también notorio para varios taxa (Orme *et al.*, 2005; Kier *et al.*, 2009). Por lo tanto en un ecosistema neotropical se pueden encontrar varias especies que se distribuyen relativamente en la misma área, siendo su estudio apropiado para detallar la historia de sus comunidades mediante filogeografía comparada (Arbeláez-Cortés, 2012; Arbeláez-Cortés *et al.* 2014).

Entre los ecosistemas mexicanos, los bosques secos del oeste del país representan focos de endemismo para varios taxa que sugieren una larga historia evolutiva exclusiva de la región (Peterson y Navarro, 2000; Ceballos *et al.*, 2002; Bradley *et al.*, 2004; Becerra, 2005). Estos bosques, aunque tienen una larga historia de intervención antrópica, representan los mayores remanentes del bosque seco neotropical, que es quizá el ecosistema más amenazado en la región (Janzen, 1988; Pennington *et al.*, 2006; Pennington *et al.*, 2009). A pesar de que su riqueza de especies es baja en comparación con otros ecosistemas neotropicales el bosque seco incluye una gran proporción de taxa endémicos y con adaptaciones únicas a este ambiente singular (Janzen, 1988; Pennington *et al.*, 2006). Esta zona se extiende por cinco de las provincias biogeográficas de México (Morrone y Marquez, 2003; Morrone, 2005) principalmente en las de la Costa Pacífica mexicana, la Sierra Madre del Sur y la Cuenca del Balsas.

Biogeográficamente, el oeste de México ha sido dividido con base en la distribución de aves (García-Trejo y Navarro, 2004; Ríos-Muñoz y Navarro-Sigüenza, 2012) y del género *Bursera* (Espinosa *et al.*, 2006). En general, para aves, hay una región al norte (Sonora-Sinaloa) y otra intermedia que abarca desde Jalisco-Colima hasta el centro de Oaxaca, que se mezcla con una zona al sur (Centro de Guerrero - Costa de Chiapas). Para *Bursera* las regiones son más discretas, pero parecen coincidir con el patrón general de las aves, llamando la atención la división de dos áreas por el Eje Neovolcánico. Para *Bursera* la depresión del Balsas es un área de endemismo que no se ha reportado en aves.

La filogeografía comparada busca congruencias en los patrones filogeográficos y en los procesos demográficos de especies que comparten, total o parcialmente, sus distribuciones geográficas. También contrasta tales patrones con información geográfica, paleoecológica o biogeográfica, basándose en la idea de que las especies que solapan sus distribuciones tienen una historia compartida. Esto se basa en la expectativa teórica de que si varias especies están co-distribuidas actualmente debieron estarlo también en el pasado, por lo cual se esperaría que los mismos eventos ecológicos o geológicos las hayan afectado en sincronía, haciendo que las historias de sus poblaciones sean semejantes (Bermingham y Avise, 1986; Joseph *et al.*, 1995; Avise, 2000; Arbogast y Kenagy, 2001; Zink, 2002; Lapointe y Rissler, 2005; Carstens y Richards, 2007; Garrick *et al.*, 2008; Castoe *et al.*, 2009; Arbeláez-Cortés, 2012).

Quizá el mayor impedimento para realizar un análisis de filogeografía comparada sea la necesidad de tener 'unidades' comparables entre diferentes especies. Un estudio ideal debería incluir el muestreo de varias especies en las mismas localidades a lo largo de toda su distribución (e.g., Garrick *et al.*, 2008). Sin embargo a pesar de que las especies presenten distribuciones comparables, sus requerimientos de microhabitat pueden hacer que no se encuentren exactamente en los mismos sitios. Una alternativa es definir 'unidades' a comparar de manera geográfica (*e.g.* poblaciones, regiones, unidades políticas, o cuadros en una gradilla) que incluyan varias muestras de las diferentes especies cuyos resultados (*i.e.* árboles filogeográficos) puedan ser luego analizados con métodos biogeográficos (Bermingham y Martin, 1998; Schneider *et al.*, 1998; Taberlet *et al.*, 1998; Sullivan *et al.*, 2000; Feldman y Spicer, 2006) o mediante superárboles (Lapointe y Rissler, 2005; Victoriano *et al.*, 2008; Weir, 2009) que permitan generar un consenso de las congruencias y diferencias entre especies. Aunque esta aproximación impide obtener los detalles que permitiría un muestreo idéntico para todas las especies, si muestra el cuadro general de la evolución reciente de una comunidad en una región geográfica.

Existen métodos para realizar árboles de especies cuyos terminales no son los haplotipos/individuos sino las unidades definidas *a priori* como especies que pueden

incluir información de varios individuos así como de diferentes marcadores moleculares (Liu *et al.*, 2008; Heled y Drummond, 2010; Yang y Rannala, 2010; Fan y Kubatko, 2011). Considero que la implementación de árboles de especies puede transferirse a la filogeografía para generar árboles de áreas como los que usualmente se usan en biogeografía. Existe consenso en que tanto las especies como las áreas, o los componentes bióticos de la biogeografía, tienen un estatus ontológico (*e.g.,* Mayr, 1987; Morrone, 2009; Crother y Murray, 2011; Crother y Murray, 2013). Es decir, son entidades discretas, reales y con historia lo cual permite que desde un punto de vista metodológico ambas puedan tratarse como terminales hipotéticos cuya identidad puede ser puesta a prueba con métodos filogenéticos como los árboles de especies. En este trabajo incluyo datos para siete especies de aves del oeste mexicano y divido la zona de estudio en áreas. Cada area la trato como un terminal para construir árboles de áreas usando un método para construir árboles de especies (Heled y Drummond, 2010; Drummond *et al.*, 2012a). Esto lo aplico a cada una de siete especies usando tanto secuencias del ADN mitocondrial (ADNmt) como del ADN nuclear (ADNn). Ya que varias de estas áreas se comparten entre especies, y en algunos casos representan linajes del ADNmt, es posible realizar una comparación directa de las relaciones filogeográficas de varias especies que es lo que procura la filogeografía comparada (Arbeláez-Cortés, 2012). Aunque no conozco ningún trabajo que haya implementado métodos de reconstrucción de árboles de especies para encontrar las relaciones de áreas a nivel filogeográfico (Arbeláez-Cortés, 2012), esta implementación es comparable a la que usualmente se hace con IMa2 (Hey, 2010) en donde se consideran las poblaciones como terminales (aunque el análisis no sea estrictamente filogenético) usándose generalmente un criterio geográfico para definir las poblaciones. Además, mi aproximación es conceptualmente comparable con los métodos biogeográficos implementados en filogeografía comparada (ver arriba) en donde los terminales usualmente representan individuos, otro tipo de entidad cuyo estatus ontológico está bien establecido.

En este trabajo, utilizo la información filogeográfica de siete especies de aves endémicas del oeste mexicano que comparten o solapan su distribución y que coinciden parcialmente en las zonas de muestreo. Para cinco especie ya he presentado análisis filogeográficos (Arbeláez-Cortés y Navarro-Sigüenza 2013; Arbeláez-Cortés *et al.*,2014; Arbeláez-Cortés *et al.*, en revisión) mientras que dos son incluidas *de novo*. Dado que mi objetivo es obtener un bosquejo de la historia reciente del oeste mexicano analizo y discuto mis resultados en un contexto biogeográfico considerando la información derivada de análisis realizados con otros taxa.

Métodos

En este trabajo incluyo siete especies de aves endémicas del oeste mexicano para las cuales obtuve tanto información del ADNmt como del ADNnuc (*Phaethornis mexicanus*, *Momotus mexicanus*, *Melanerpes chrysogenys*, *Pheugopedius felix*, *Thryophilus sinaloa*, *Vireo hypochryseus* y *Passerina leclancherii*). Todas las muestras analizadas son del Museo de Zoología de la Facultad de Ciencias de la Universidad Nacional Autónoma de México (MZFC-UNAM) excepto dos muestras de sangre de *P. felix* que corresponden a la colección de sangre de Borja Milá en el Museo Nacional de Ciencias Naturales de Madrid. La obtención de ADN, la amplificación de regiones mediante PCR así como la obtención y edición de secuencias se realizaron con los mismos protocolos indicados en Arbeláez-Cortés y Navarro-Sigüenza (2013), Arbeláez-Cortés *et al.*, (2014) y en Arbeláez-Cortés *et al.*, (en revisión). Para *P. felix y T. sinaloa* incluyo 103 secuencias del COI y 109 muestras para las cuales se obtuvo al menos uno de los cuatro marcadores nucleares (20454, GAPDH, MUSK & TGFB). La Figura 1 muestra la cobertura del muestreo de este estudio.

Dado que mi intención es hacer una comparación directa de la variación genética de las siete especies, dividí la zona de estudio en nueve regiones así: 1) Sonora-Chihuahua-SinaloaN, 2) Sinaloa-Nayarit-JaliscoN, 3) Islas Tres Marías, 4) Jalisco-Colima-MichoacánW, 5) MichoacánE-GuerreroW, 6) Balsas, 7) GuerreroE, 8) OaxacaW y 9) OaxacaE. Cada región fue delimitada considerando dos razones: 1) que incluyeran secuencias del ADNmt, y al menos, un locus del ADNn de dos o más especies. 2) que representaran áreas con cierto sentido biogeográfico, es decir que hayan sido identificadas como áreas de endemismo o pertenezcan a alguna división biogeográfica (García-Trejo y Navarro, 2004; Morrone, 2005), incluyan un haplogrupo de alguna de las especies o que estén divididas por alguna barrera geográfica. Las nueve regiones se presentan en la Figura 2.

Seleccioné los marcadores moleculares que tuvieran la mayor cobertura geográfica y eliminé cualquier marcador que no estuviera presente en al menos una región donde se encontrara la especie. De esta manera el grupo de datos usado para algunas especies resultó menor al presentado en los capítulos anteriores (e.g., *V. hypochryseus* se analizó solo para el ND2 y el GAPDH) pero como ya indiqué siempre incluí ADNmt y al menos un marcador del ADNn. Para *P. felix* excluí de los análisis dos *indels* que encontré en el GAPDH ya que no pude resolver la fase de dichos alelos con certeza.

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Análisis de datos

Utilicé *BEAST (Heled y Drummond, 2010; Drummond *et al.*, 2012a; Drummond *et al.*, 2012b) para determinar las relaciones entre regiones de acuerdo con la información molecular de cada especie. Utilicé MrModeltest (Nylander, 2004) para definir el modelo

de sustitución de cada marcador en cada especie y definí la frecuencia de bases como *empirical*. El modelo de reloj molecular empleado fue el *log normal relaxed uncorrelated molecular clock* y la tasa de sustituciones / sitio / año fueron las siguientes: 2.9×10^{-8} para el ND2 (Lerner *et al.*, 2011), 2.07×10^{-8} para el CytB (Weir y Schluter, 2008) (Weir Passeriformes), 1.6×10^{-8} para el COI (Lerner *et al.*, 2011), 1.67×10^{-9} para el 20454 (Lim y Sheldon, 2011, calculado para un marcador similar), 1.2×10^{-9} para el GAPDH (Lerner *et al.*, 2011), 1.7×10^{-9} para el TGFB (Lerner *et al.*, 2011) y 1.7×10^{-9} para el MUSK que no ha sido calculado para este intrón en particular pero si para otro intrón (TGFB). El modelo de especiación fue el de Yule y empleé un árbol UPGMA para iniciar las búsquedas. La búsqueda incluyó 200.000.000 MCMC, muestreando topologías y parámetros cada 2000 generaciones. Los tiempos de divergencia entre las áreas se presentan junto con sus intervalos de confianza con el fin de establecer un marco temporal de referencia para descartar eventos históricos. No obstante, dado que algunas de estas áreas no representan entidades reales para algunas especies puede ser inapropiado calcular sus tiempos de divergencia. Por lo tanto, incluyo también la estimación de los tiempos de divergencia para los haplogrupos mayores de cada especie (*i.e.,* la mayor divergencia filogeográfica) usando también *BEAST con un grupo más completo de loci (ver capítulos anteriores).

Si las áreas incluidas como terminales hipotéticos en el análisis representan unidades filogeográficas, estas deberían diferenciarse de las demás áreas en el análisis filogenético, de otra manera aparecerían como terminales de una politomia. Para esto, utilicé el programa Densitree (Bouckaert, 2010) que permite visualizar la concordancia encontrada tanto entre las topologías como en los tiempos de divergencia de los árboles guardados durante las búsquedas en *BEAST.

De existir congruencia entre las relaciones de las áreas de las diferentes especies, se esperaría que su consenso tuviera una topología resuelta. Para verificar esta hipótesis, utilicé el software Clann (Creevey y McInerney, 2005; Creevey y McInerney, 2009) que permite hacer superárboles empleando el método de *Matrix Representation using Parsimony* (MRP). Primero realicé una matriz Baum-Ragan a la que le añadí una fila con un grupo externo codificado como ceros. Esta matriz la analicé usando parsimonia en Winclada (Nixon, 2002) con 10,000 repeticiones, 1000 puntos de partida y 100,000 árboles en memoria.

Finalmente, si la historia de las especies en la zona ha sido compartida, deberían recuperarse patrones en la diversidad genética de todas las especies. Por lo tanto calculé la diversidad genética (π) en cada una de las regiones, para cada loci de cada especie, y la grafiqué con el fin de identificar si existe alguna tendencia geográfica de la diversidad genética.

Resultados

El análisis de los superárboles produjo 32 árboles, de 13 pasos, igualmente parsimoniosos. Las topologías obtenidas en los arboles de áreas varió entre especies (Figuras 3 y 4); no obstante se pueden observar en el superárbol ciertas congruencias en la relación entre áreas (Figura 3A). Por ejemplo, las áreas en ambos extremos de la zona de estudio se agruparon en sendos clados: Sureste (OaxacaE,OaxacaO) y Noroeste ((Sinaloa-Nayarit-JaliscoN, Islas Tres Marias),Sonora-Chihuahua-SinaloaN). Por su parte, las cuatro áreas intermedias no tuvieron relaciones resueltas en el superárbol. De esta manera la congruencia topológica de las siete especies es solo parcial. Es decir: únicamente algunas relaciones entre áreas se comparten entre dos o más especies. Otras áreas que no estuvieron resueltas en el superárbol, como el Balsas, que incluyó seis de las siete especies, mostró diferentes relaciones con otras áreas dependiendo de la especie analizada. Por su parte el área de GuerreroE que se presentó en cinco de las siete especies mostró una tendencia a agruparse con las áreas de Oaxaca pero esta relación no estuvo bien soportada en todas las especies (Figura 3).

El árbol de áreas de *P. mexicanus* (Figura 3B) fue el único que no presentó estructura topológica. Los marcadores moleculares usados para esta especie no identificaron ningún tipo de asociación clara entre las cinco áreas donde se encontró a la especie. En contraste, los arboles de áreas obtenidos para las demás especies presentaron entre dos y cuatro divisiones claras. *Momotus mexicanus* (Figura 3C) presentó una división mayor entre las dos áreas del norte y las demás áreas (ubicadas entre Guerrero y Oaxaca). *Melanerpes chrysogenys* (Figura 3D) también presentó esta división entre las dos áreas del norte y las demás, pero además las otras cuatro áreas se dividieron en dos grupos. *Vireo hypochryseus* (Figura 3E) presentó una división mayor entre las áreas del sur y las del norte, pero el área de Jalisco-Colima-MichoacánW, que es geográficamente intermedia, mostró relación con los dos grupos mayores. El árbol de áreas de *P. leclancherii* (Figura 3F) presentó cuatro divisiones claras, estando las áreas del sur (OaxacaW y OaxacaE) agrupadas en un solo clado y las dos áreas del norte formando otro clado. El área de GuerreroE estuvo más asociada con el clado que incluye ambas áreas de Oaxaca, pero muestra cierta relación también con áreas del norte. Por otro lado, *T. sinaloa* (Figura 3G) presentó una división mayor entre dos grupos de áreas, pero el grupo del norte parece presentar una división secundaria del área de Jalisco-Colima-MichoacánW con respecto a las dos áreas del norte. Finalmente, *P. felix* que fue la especie que estuvo presente en el mayor número de áreas mostró un árbol (Figura 3H) con una división mayor de las áreas en dos grupos geográficamente coherentes (*i.e.,* áreas al norte vs áreas al sur), pero ambos grupos están subdivididos. En el grupo de las áreas al sur las dos áreas de

Oaxaca formaron un grupo diferente del Balsas. El área de GuerreroE apareció separada pero se relacionó con las áreas al sur (OaxacaE, OaxacaW y Balsas) y al norte (Jalisco-Colima-MichoacanW). A pesar de que las tres áreas que conforman el grupo del norte presentaron ciertas diferencias entre sí, sus relaciones no se resolvieron.

De acuerdo con la evidencia molecular, la divergencia genética entre las áreas en el oeste mexicano incluidas en este estudio, se podría extender hasta 400.000 años atrás (Figura 4). No obstante, la mayoría de las divergencias se circunscriben a los últimos 100.000 años (Figura 4). La división más profunda en la mayoría de las especies se da entre las áreas al norte con respeto a las demás. No obstante, estas áreas no siempre son las mismas. Por ejemplo, en algunos casos incluyen solo las áreas al norte del Eje Neovolcánico (*P. felix* y *V. hypochryseus*) y en otros casos incluye también a Jalisco-Michoacán (*M. mexicanus*, *M. chrysogenys* y *T. sinaloa*). Las excepciones son *P. mexicanus* que no presenta ninguna división mayor y *P. leclancherii* que tiene una distribución más restringida que las otras especies.

La diversidad genética de las especies en cada una de las áreas no presentó ninguna tendencia clara (Figura 5). En general, la diversidad nucleotídica de los marcadores tanto nucleares como mitocondriales estuvo entre 0 y 0.014 para cada área. Los valores más altos para algunos marcadores se observaron en GuerreroE, Balsas y en Jalisco-Colima-Michoacán pero no corresponden a un patrón de mayor diversidad en esas áreas ya que otros marcadores, o especies, tuvieron también valores bajos en estas mismas áreas.

Discusión

En este estudio muestro que las siete especies analizadas presentan una estructura filogeográfica para al menos los marcadores mitocondriales y que en la mayoría existe cierto grado de estructura geográfica en algunos loci nucleares. Este resultado indica que el oeste de México es una región evolutivamente activa, donde pudieron haber ocurrido diferentes procesos de vicarianza y reducción de flujo génico entre poblaciones. No obstante, la estructura filogeográfica de las siete especies solo presenta una congruencia parcial.

La congruencia topológica total es el resultado teórico de una comunidad que ha evolucionado concertadamente a lo largo del tiempo en la cual cada especie respondió del mismo modo a los cambios ambientales ocurridos en una región (Bermingham y Avise, 1986; Zink, 2002; Lapointe y Rissler, 2005; Morrone, 2009). Sin embargo, los resultados empíricos de los estudios de filogeografía comparada generalmente presentan cierta incongruencia entre las especies comparadas (Arbeláez-Cortés,

2012), poniendo de manifiesto que tanto las idiosincrasias en la biología de cada especie como los procesos históricos en una zona tiene un papel en los patrones de la variación genética. El debate que existe entre una propuesta de repuesta individualista (a nivel de especie) y otra de una respuesta colectiva (a nivel de comunidad) no se limita a la biogeografía, sino que ha estado presente en la ecología por más de un siglo (Vegas-Vilarrúbia *et al.*, 2011). Sin embargo, considerar sólo una de las dos alternativas es ingenuo cuando se trata con un fenómeno complejo como la evolución biológica. De manera que la congruencia entre patrones filogeográficos debe verse como parte de un continuo (Arbeláez-Cortés, 2012) especialmente cuando se trata de comunidades neotropicales que tienen una gran diversidad taxonómica y ecológica.

A pesar de que los aspectos metodológicos (*i.e.,* diferente muestreo entre especies) pueden explicar parte de la incongruencia, considero que los aspectos biológicos (*i.e*., respuesta diferencial de las especies a los mismos cambios ambientales) son más relevantes en este caso. Propongo esto basandome en el hecho de que mi comparación directa de dos especies con un muestreo y tolerancias ambientales similares (*P. leclancherii* y *M. chrysogenys*, Arbeláez-Cortés *et al.*, 2014) no soportaron completamente la hipótesis de congruencia en sus diferencias genéticas. Esto pone de manifiesto que las diferencias en la historia natural (*e.g*., hábitos arbóreos vs forrajeo en el suelo) de cada especie pueden estar involucrados. Esto ya ha sido indicado para explicar la variación en las diferencias genéticas de aves en los bosques húmedos de Sur América (Burney y Brumfield, 2009).

Ahora bien, resulta interesante que a pesar de la existencia de incongruencia entre los patrones filogeográficos de las especies, haya ciertas coincidencias. Por ejemplo, la existencia de una disrupción filogeográfica alrededor de las estribaciones costeras del eje Neovolcánico, así como en la zona entre el sur de Jalisco y el borde de Michoacán-Guerrero y en la zona entre el centro de Guerrero y el borde Guerrero-Oaxaca. Una o varias de estas zonas ya se han identificado como disrupciones filogeográfica en otros organismos (Zaldívar-Riverón *et al.*, 2004; Mateos, 2005; Miller y Schaal, 2005; Devitt, 2006; Mulcahy, 2008; Zarza *et al.*, 2008; Pringle *et al.*, 2012, Arbeláez-Cortés *et al*. 2014). Para detalles ver la figura 1 presentada en Arbeláez-Cortés *et al*. (2014). Además, también existen especies hermanas de vertebrados que presentan distribuciones separadas por alguna de estas zonas (Howell y Webb, 1995; Daza *et al.*, 2009) mientras que un estudio biogeográfico con aves ha reportado recambio de especies en, o cerca a, estas zonas (García-Trejo y Navarro, 2004). Esta concordancia entre disrupciones filogeográficas y zonas de diferenciación biogeográfica parece reflejar una estructura jerárquica de la distribución geográfica de la biodiversidad que ya ha sido notada (Avise, 2000; Morrone, 2009) pero poco explorada. Adicionalmente, el área del Balsas que resultó tener linajes diferenciados para otros taxones (Zaldívar-Riverón *et al.*, 2004; Espinosa *et al.*, 2006) parece tener relación filogeográfica distinta dependiendo de la especie estudiada. Esto se asemeja a la naturaleza de zona de

transición biogeográfica que se le ha asignado en algunos estudios (Morrone, 2005). La semejanza entre patrones geográficos de las comunidades y de los alelos intraespecíficos lleva a pensar en la importancia biogeográfica de las zonas indicadas que pudieron haber funcionado como rupturas biogeográficas en diferentes momentos durante la larga historia de la región.

Una característica que más o menos se comparte entre estas zonas con disrupción filogeográfica en el oeste de México es que presentan elevaciones de más de 1900 m a menos de 30 km de la costa (Arbeláez-Cortés *et al.* 2014). La presencia de esas montañas sugiere que ciertos procesos geológicos pudieron afectar las biotas (*e.g.,* Mateos, 2005; Devitt, 2006). Sin embargo, los eventos geológicos mayores en la zona ocurrieron hace más de 3 millones de años (Morán-Zenteno *et al.*, 2000; Becerra, 2005), y dado que la datación molecular indica que la diferenciación intraespecífica en las siete especies ha ocurrido durante los últimos 400.000 años se pueden descartar los procesos geológicos como los factores principales. Además de estos factores, los cambios climáticos también pudieron generar cambios de la distribución de las especies disminuyendo el flujo génico entre sus poblaciones y promoviendo así la diferenciación genética. En particular para el centro y oeste de México hay evidencia paleoecológica y paleoclimática que indica cambios tanto en la temperatura como en la humedad durante los ultimos 35.000 años, y que promovieron cambios en la vegetación, la cual mostró descensos altitudinales de hasta 1000 metros con respecto al presente (Berrio *et al.*, 2006; Ortega-Rosas *et al.*, 2008a; Ortega-Rosas *et al.*, 2008b; Caballero *et al.*, 2010; Ortega *et al.*, 2010; Roy *et al.*, 2012; Stevens *et al.*, 2012; Lachniet *et al.*, 2013; Lozano-García *et al.*, 2013). A pesar de que esta evidencia es reciente en comparación con los tiempos de divergencia que reporto, la existencia de eventos climáticos que afectaron la vegetación en el oeste mexicano en su historia descarta la estabilidad de la distribución del bosque seco y permite pensar en cambios similares en épocas mucho más antiguas.

Propongo que las zonas montañosas cercanas la costa (y las tierras bajas aledañas) pudieron haber sido zonas de inestabilidad climática donde la vegetación cambió de bosque seco a vegetación más asociada con una mayor humedad (*e.g*., bosques mesofilos o selvas humedas). Este escenario es parcialmente soportado por los modelos de nicho ambiental de algunas de las especies que fueron proyectados en las condiciones climáticas del pasado (Arbeláez-Cortés *et al.*,2014; Arbeláez-Cortés *et al.* en revisión) y por evidencia paleoclimática y paleoecológica que apesar de ser reciente indica la ocurrencia de climas distintos que afectaron la distribución y posiblemente la conección del bosque seco (Berrio *et al.*, 2006; Ortega-Rosas *et al.*, 2008a; Ortega-Rosas *et al.*, 2008b; Caballero *et al.*, 2010; Ortega *et al.*, 2010; Roy *et al.*, 2012; Stevens *et al.*, 2012; Lachniet *et al.*, 2013; Lozano-García *et al.*, 2013).

Mi trabajo indica una diversificación activa de linajes endémicos en la parte norte del bosque seco neotropical, y refuerza la idea de que el oeste de México es una región con un alto grado de endemismos, alberga numerosos taxa con diversas historias, y es así un área importante en la cual estudiar la diversificación reciente de las biotas neotropicales. Además, la existencia de zonas de diferenciación biogeográfica en o cerca a las zonas identificadas aquí como de disrupción filogeográfica sugiere que diferentes procesos han tenido un papel en la diferenciación de la biota del oeste de México. Los resultados de este trabajo también llevan a plantear la pregunta acerca del tipo de cambios ocurridos en la zona y que promovieron la diferenciación filogeográfica en especies que muestran cierto grado de tolerancia a modificaciones antrópicas del paisaje. Los resultados de este estudio van más allá de representar un caso regional ya que son comparables con los obtenidos en otros estudios realizados en ecosistemas tropicales que como este, tienen una distribución alargada en dirección norte-sur y están bordeados por montañas y por el mar. Tales son los casos del bosque húmedo del este de Australia, del bosque atlántico de Brasil y de algunos ecosistemas en Centro América (Joseph *et al.*, 1995; Schneider *et al.*, 1998; Carnaval *et al.*, 2009; Moussalli *et al.*, 2009; Martins, 2011; Poelchau y Hamrick, 2013) para los cuales las especies estudiadas exhiben generalmente estructura filogeográfica que son más o menos comparables entre especies simpátricas. Esto permite pensar que ciertos atributos geográficos de estas regiones pueden estar relacionados con una alta tasa de diversificación reciente de linajes debido a fluctuaciones climáticas, y sería una alternativa para explorar la generalidad de los procesos involucrados en la historia de ecosistemas tropicales que comparten ciertos rasgos geográficos y que son centros de endemismo de especies.

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Leyendas de las figuras

Figura 1. Localidades con muestreo de individuos de siete especies de aves del oeste de México. Cada color representa una especie diferente y cada símbolo un loci distinto. Para detalles sobre el muestreo de las especies se refiere al lector a los capítulos anteriores y al Apéndice de este capítulo.

Figura 2. Áreas geográficas definidas para los análisis de siete especies de aves del oeste de México

Figura 3. Superárbol de las relaciones entre áreas y *densitrees* indicando el consenso de las relaciones entre áreas de cada una de las siete especies de aves del oeste de México. B) *Phaethornis longirostris*, C) *Momotus mexicanus*, D) *Melanerpes chrysogenys*, E) *Vireo hypochryseus,* F) *Passerina leclancherii* G) *Thryophilus sinaloa* y H) *Pheugopedius felix*.

Figura 4 .Marco temporal de la divergencia entre áreas de acuerdo con datos moleculares de siete especies de aves del oeste de México. El asterisco indica el tiempo de datación para la divergencia filogeográfica mas profunda de cada especie (i.e., haplogupos mayores). Este fué calculada usando un set de datos mas completo al usado para determinar las áreas. Las barras grises de los nodos indican los intervalos de confianza de los datajes. Los colores en los terminales son los colores con los que se representaron las áreas en la Figura 2.

Figura 5. Patrones de variación de la diversidad genética (π) de diferentes loci de de siete especies de aves del oeste de México de acuerdo con nueve regiones geográficas definidas *a priori* (ver Fig. 2). Cada símbolo representa una especie diferente: *P. mexicanus* = rectangulo vertical, *M. mexicanus* = rombo, *M. chrysogenys* = cruz, *V. hypochryseus* = triangulo lleno, *P. leclancherii* = triangulo vacio, *T. sinaloa* = cuadrado lleno y *P. felix* = cuadrado vacio.

Figura 1

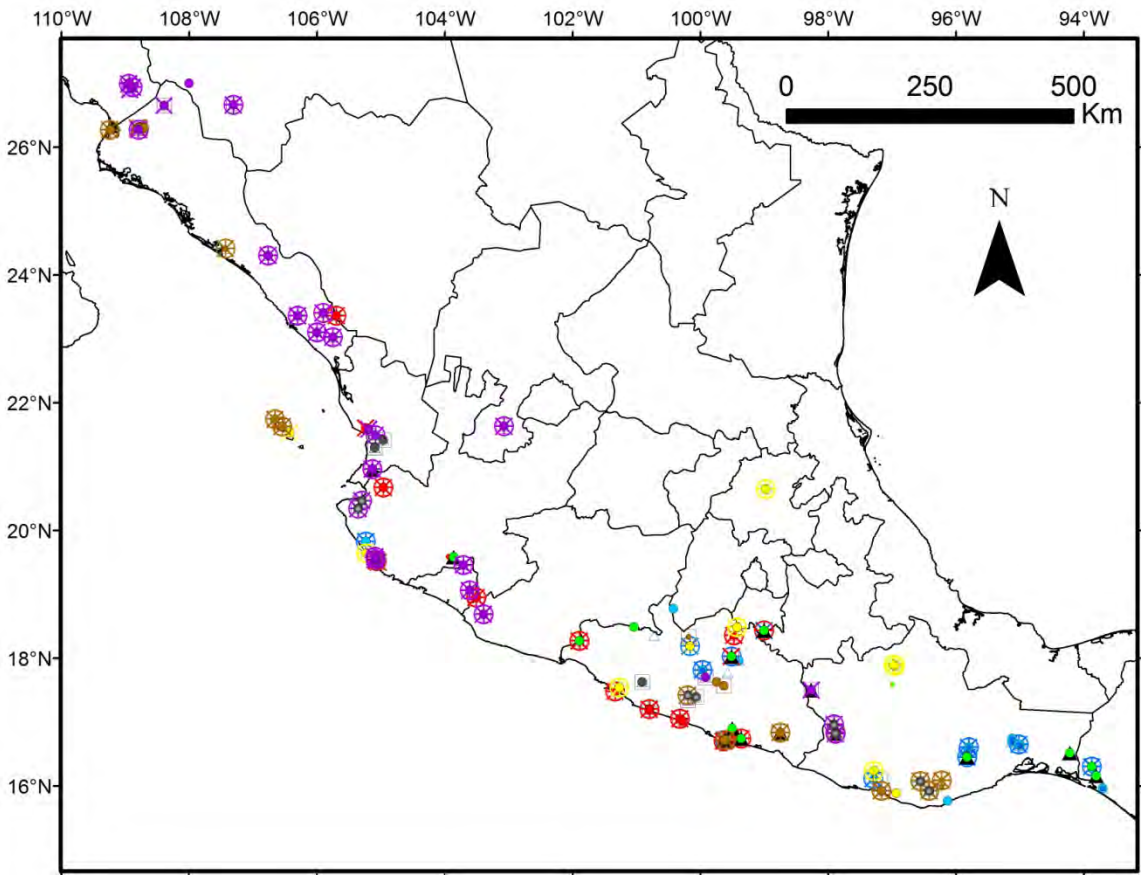
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Figura 2

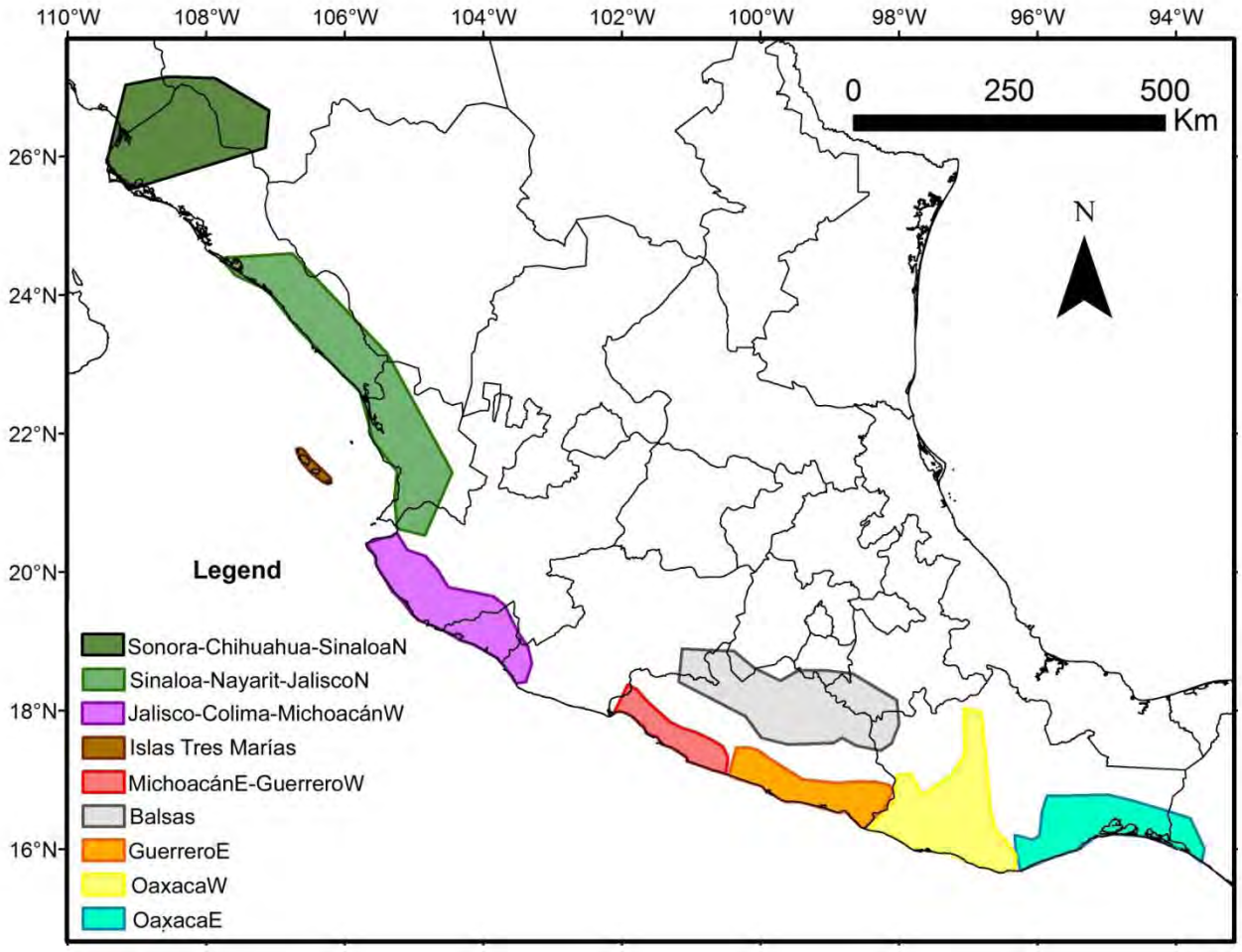
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Figura 3

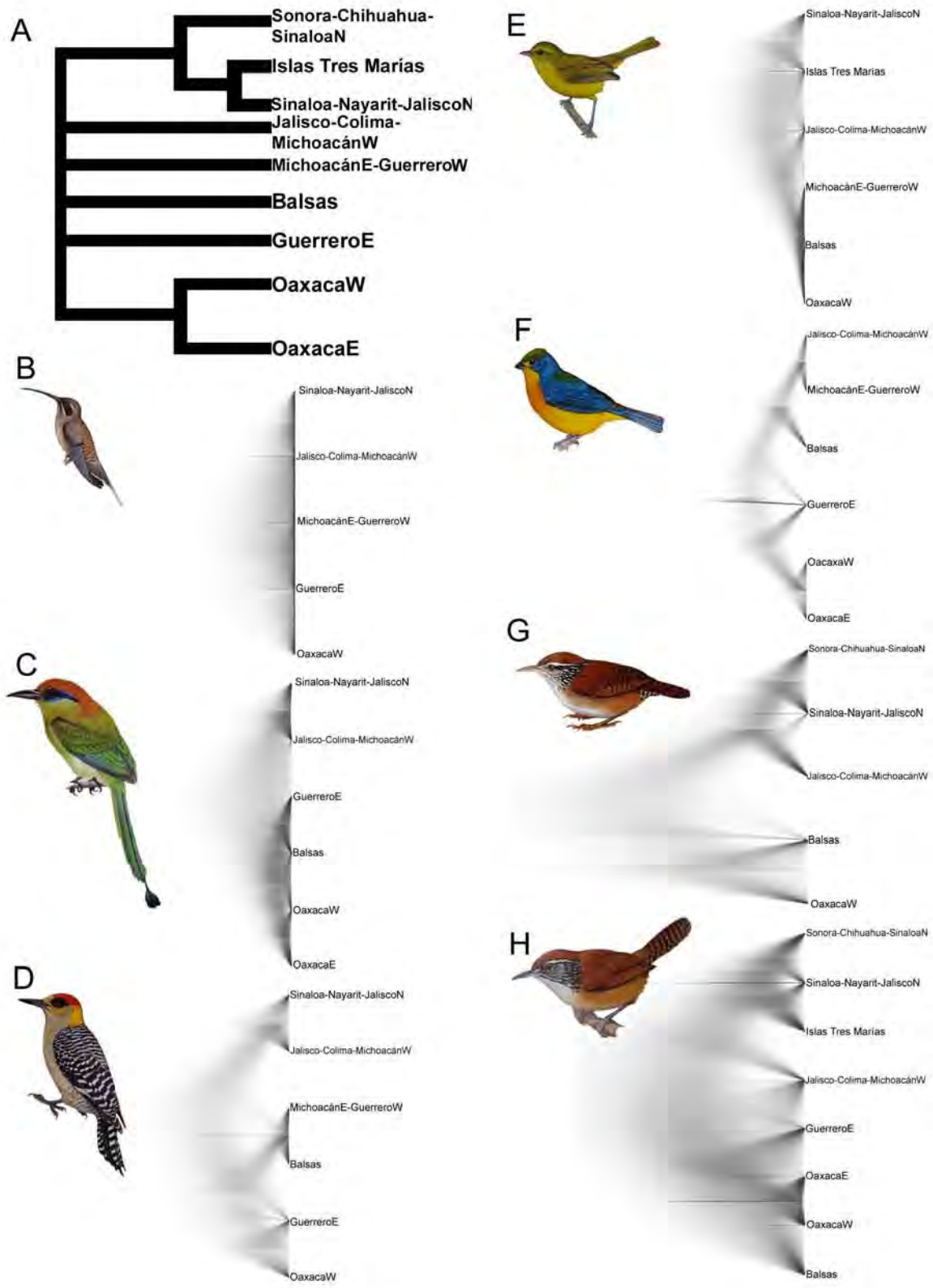
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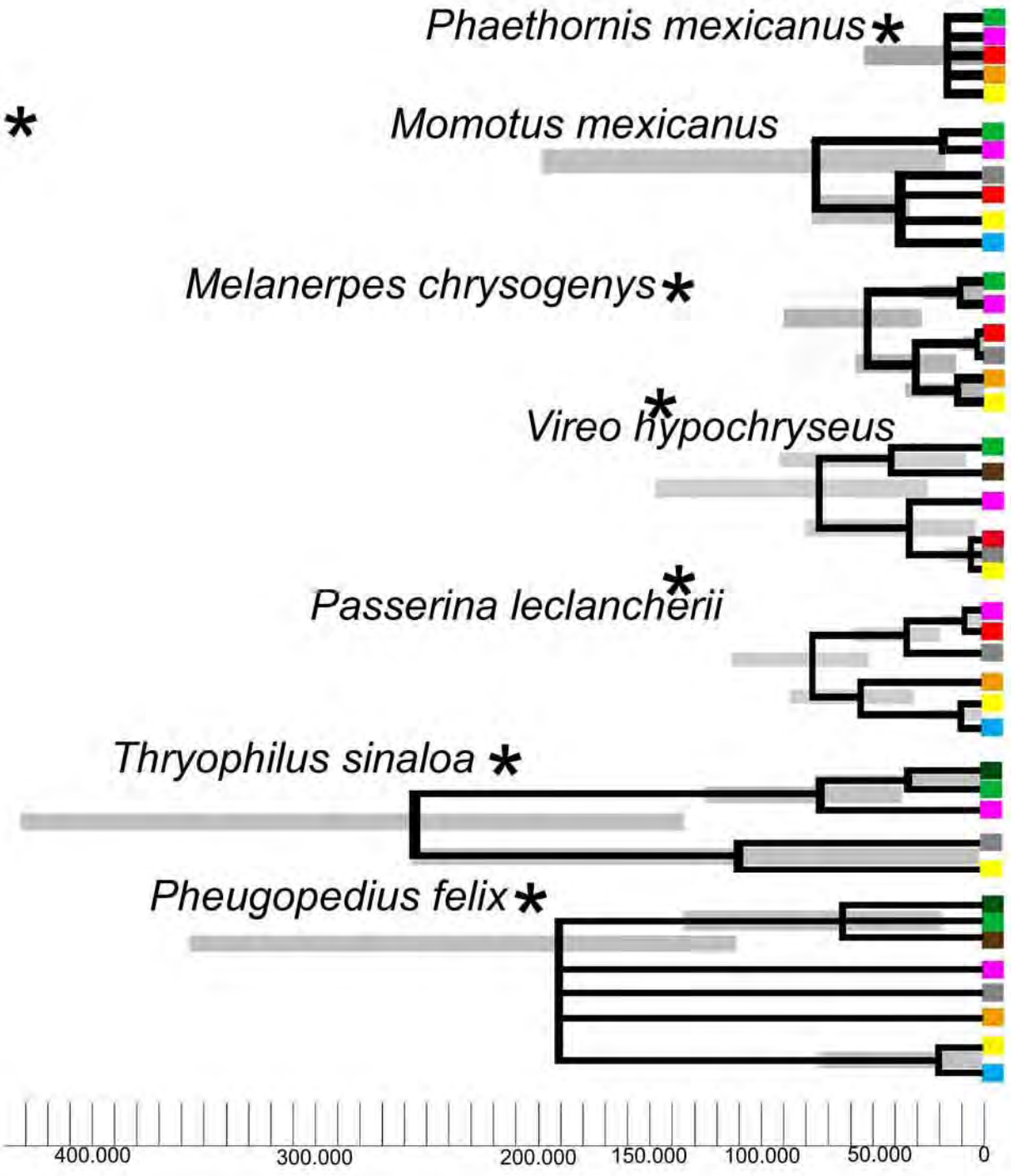
Figura 4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Passerina leclancherii *
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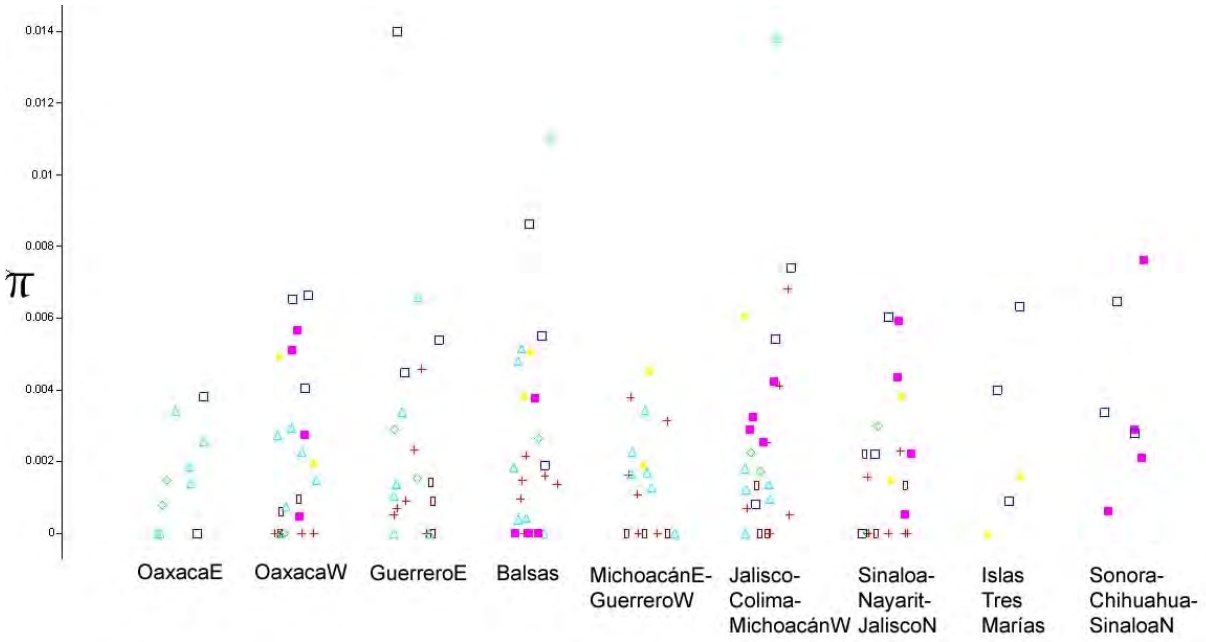
Figura 5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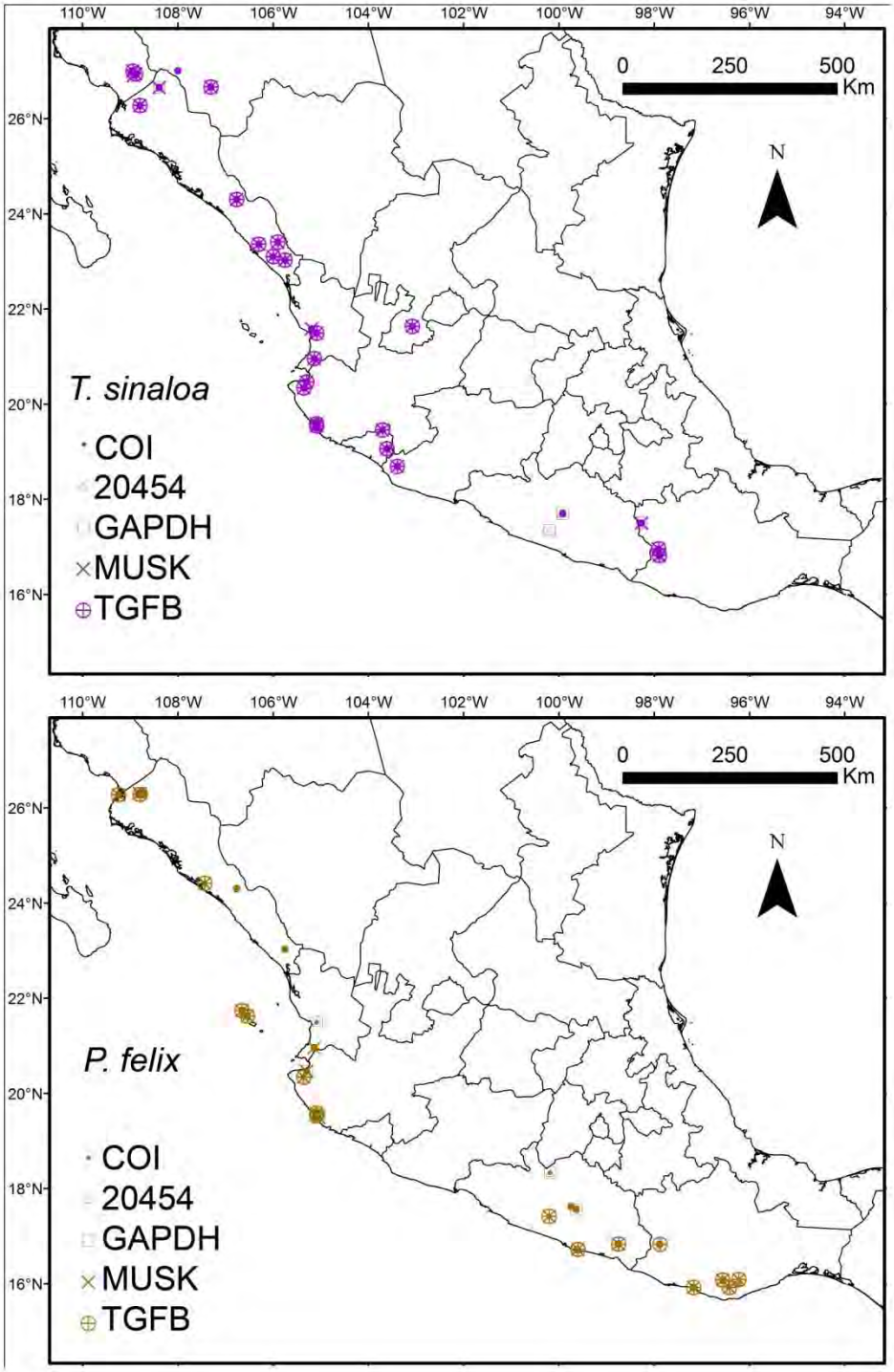
Apéndice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DISCUSIÓN GENERAL Y CONCLUSIONES

En este estudio he mostrado que las siete especies analizadas presentan estructura filogeográfica en los marcadores mitocondriales y que en la mayoría existe cierto grado de estructura geográfica en algunos loci nucleares [25-27, 81]. Este resultado coincide con lo encontrado en otros taxa estudiados en la zona [36-38, 40, 42, 43, 85]. La existencia de estructura filogeográfica en aves endémicas del oeste de México complementa los patrones biogeográficos y filogenéticos de otros taxa que previamente habían indicado la existencia de una subdivisión de la biota en esta región [19, 75-77, 86-88]. Toda esta evidencia indica que el oeste de México, además de ser un centro de endemismo, es una región evolutivamente activa, donde diferentes procesos de vicarianza y reducción de flujo génico entre poblaciones generaron la evolución de varios linajes. No obstante, la estructura filogeográfica de las diferentes especies solo presenta una congruencia parcial, sugiriendo que cada especie ha tenido una respuesta idiosincrática a los procesos históricos que han ocurrido en la zona.

En los estudios de filogeografía comparada, la congruencia topológica total es el resultado teórico de una comunidad que ha evolucionado concertadamente a lo largo del tiempo y en la cual cada especie respondió del mismo modo a los cambios ambientales ocurridos en la región [4, 7, 89-92]. Sin embargo, el resultado empírico de los estudios filogeográficos muestra que en general las especies presentan patrones incongruentes o solo parcialmente congruentes [10, 93-102]. La ausencia de congruencia topológica total entre patrones filogeográficos de especies co-distribuidas puede ser el resultado de factores tanto biológicos como metodológicos [4]. A pesar de que estos últimos pueden relacionarse parcialmente con la incongruencia que encontré, considero que los aspectos biológicos (*e.g.,* respuesta idiosincrática de las especies a los mismos cambios ambientales) son más relevantes en este caso. Esta idea es soportada por el hecho de que la comparación directa de dos especies (*P. leclancherii* y *M. chrysogenys*) con un muestreo similar y que pueden encontrarse en hábitats similares en la región donde se solapan sus distribuciones y con tolerancias climáticas similares [25] no soportaron completamente la hipótesis de

congruencia entre sus diferencias genéticas. A pesar de la existencia de incongruencia entre los patrones filogeográficos de las especies, hay ciertas coincidencias en puntos particulares [25, 81].

Quizá la característica fisiográfica más evidente a lo largo de la costa del pacífico mexicano sean las estribaciones del Eje Neovolcánico, con elevaciones de más de 1900 m muy cerca de la costa en los límites entre Nayarit y Jalisco. Seis de las especies analizadas se distribuyen en esta área, sin embargo solo dos (*P. felix* y *V. hypochryseus*) muestran un haplogrupo restringido al norte de esta zona, lo que es similar a lo encontrado para el pez *Poecilia butleri* [36], para *Rana forrieri* [35], y para los reptiles *Hypsiglena torquata* [43], *Trimorphodon biscutatus* [37] y *Ctenosaura pectinata* [38]. En contraste, las otras especies de aves endémicas muestran un haplogrupo que se distribuye tanto al norte del estas estribaciones como hacia el sur y que en ciertos casos alcanza el límite entre Michoacán y Colima.

La existencia de una disrupción filogeográfica alrededor de las estribaciones costeras del eje Neovolcánico ha sido explicada por la actividad geológica de hace mas de 10 millones de años [37], el vulcanismo de hace 3 a 6 millones de años[36, 38], y de una expansión reciente a través de esta zona, como es el caso de *H. torquata* [43]. Para *V. hypocryseus* y *T. felix* el tiempo estimado para la diferenciación de los haplogrupos a ambos lados de esta zona fue durante los últimos 130.000 años, lo que es muy reciente para considerar que los eventos geológicos fueron los responsables de la diferenciación. Las demás especies quizá se hayan expandido a través de estas estribaciones pero la dirección de dicho cruce no es clara con los datos disponibles. Vale la pena anotar que *T. felix* y *V. hypochryseus* tienen poblaciones en las Islas Tres Marias, que junto con las poblaciones al norte del eje Neovolcánico, forman un haplogrupo. Esto es comparable con lo encontrado para *Cardinalis cardinalis* [15] y para *Icterus pustulatus* [16], cuyas poblaciones insulares también se encuentran más relacionadas con las poblaciones al norte del Eje Neovolcánico que con otras poblaciones continentales, sugiriendo que la colonización de las islas Tres Marias ocurrió después de la separación poblacional a ambos lados del eje Neovolcánico.

Siguiendo hacia el sur, se encuentra que cinco especies (*P. mexicanus*, *M. mexicanus*, *M. chrysogenis T. felix* y *T. sinaloa*) presentan una disrupción filogeográfica en la zona

entre el sur de Jalisco y el borde de Michoacán-Guerrero. No obstante, existe un vacío en el muestreo de varias especies para esta zona que impide identificar con certeza si se trata de una zona de hibridación (como lo sugiere la distribución de haplotipos de *M. chrysogenys*) o si existe un área definida de disrupción marcada. Esta zona también representa una disrupción filogeográfica en el ADNmt de la hormiga *Azteca pittieri* pero no en su ADNn [40], así como en *C. pectinata* [38] y parece relacionarse con la especiación de serpientes [55, 56], estando además cerca de una zona de diversificación del género *Bursera* [19, 87]. La existencia de disrupción filogeográfica en esta zona (al menos en el ADNmt) indica la separación de las poblaciones pero no se ha propuesto ningún proceso histórico que lo explique. En el caso de la especiación en serpientes se considera que la formación de la cuenca del rio Balsas, que cruza la zona, o cambios climáticos durante el Mioceno pudieran estar involucrados [55, 56]. Como ya mencioné para las estribaciones del Eje Neovolcánico, en Michoacán también se encuentran algunas zonas montañosas de más de 1900 m cercanas a la costa (Sierra de Coalcomán) que posiblemente se relacionen con la ocurrencia de diferenciación filogeográfica en las aves endémicas. Pero la ubicación precisa de una zona de disrupción filogeográfica requiere de un muestreo más completo.

Siguiendo hacia el sureste se hace claro que la zona entre el centro de Guerrero y el límite entre Guerrero-Oaxaca representan otra zona de disrupción filogeográfica para *P. leclancherii, M. chrysogenis, P. felix* y *M. momota*; comparable a la que se ha documentado para otras especies [35, 37, 38, 40, 42]. Esto indica la existencia de fragmentación y aislamiento de las poblaciones, pero no se ha relacionado con un proceso histórico que permita explicarlo. En esta zona existen algunos accidentes geográficos tales como sistemas de lagunas costeras y el rio Papagayo, pero aunque en esta zona la sierra Madre del Sur se aproxima a la costa, las zonas montanas de más de 1500 m a menos de 30 km de la costa se encuentran en el suroeste de Oaxaca a unos 90 km del borde entre Oaxaca y Guerrero.

La datación molecular indica que la diferenciación intraespecífica en las siete especies ha ocurrido durante los últimos 500.000 años y principalmente en los últimos 150.000 años. Este marco temporal coincide con la época de cambios climáticos del Pleistoceno [103]

que se ha asociado con especiación y con el origen de variación intraespecífica de diferentes taxa neotropicales [8, 9].

Existen evidencias paleoclimáticas, paleoecológicas, y arqueológicas que indican que en el oeste de México han ocurrido cambios ambientales durante los últimos 35.000 años. Además, algunos estudios sobre el ecosistema de bosque seco en Sur América sugieren cambios históricos en este ecosistema. Estas evidencias son las siguientes: 1) Condiciones climáticas en el centro de México, hace 35.000 años, fueron similares a las actuales volviéndose más secas hacia 20.000 años en el pasado para volver a ser húmedas después, de acuerdo con un análisis de isótopos en caracoles [104]. 2) Disminuciones en temperatura de hasta 8°C hace 25.000 años para el Eje Neovolcánico con descenso de hasta 1000 m en la elevación de la línea del glacial y de los cinturones de vegetación [67, 105] que pudieron afectar también los ecosistemas de tierras bajas. 3) Temperaturas bajas y mayor precipitación hace 24.000 años en el noroeste de México de acuerdo con análisis de sedimentos de un paleo-lago en Chihuahua [106]. 4) Fluctuaciones en la precipitación de los veranos (*i.e*., monzón) durante los últimos 22.000 años que alcanzaron un máximo hace 10.000 años de acuerdo con análisis de estalagmitas en el suroeste de México [107]. 5) Mayor separación de los bosques secos de Sur América durante el Último Máximo Glacial (hace 21.000 años) de acuerdo a reconstrucciones usando ENMs [108]. 6) Cambios marcados en la composición de especies de algunos bosques secos en Sur América y relativa estabilidad de otros durante los últimos 18.000 años de acuerdo con registro paleopalinológico[109]. 7) Condiciones más secas, hace 15.000 años, [110] y cambios en las comunidades vegetales asociados a cambios climáticos durante los últimos 11.500 años [105] de acuerdo con la evidencia de un lago a 2000 m en Michoacán-Guanajuato. 8) Cambios en los cinturones altitudinales de vegetación, con presencia de bosques de Pinos a 1500 m en la Sierra Madre Occidental, hace 13.000 años, que actualmente se encuentran principalmente arriba de 1800 m [71, 111]. 9) Reemplazo del bosque seco por bosques más húmedos o por vegetación de sabana durante los últimos 9600 años [74, 112, 113]. 10) Presencia de bosques de pinos (7000 – 5000 años atrás) e incursiones marinas (hace 5500 años) en la planicie costera de Sinaloa [72]. 11) Presencia de polen de *Pinus* y *Quercus* hace entre 5300 y 2700 años en la costa de Sonora [114]. 12) Asentamientos humanos en Sonora hace 4700 años [115]. 13) Evidencia de sedimentos para la cuenca del

río Balsas que indican que durante los últimos 2700 años se ha sucedido periodos de 1000 años en los que el bosque seco ha sido reemplazado por vegetación de bosque mesófilo que luego ha vuelto a ser reemplazado por bosque seco [74].

A pesar de que la bibliografía documenta procesos históricos dispersos y relativamente recientes en comparación con los eventos de divergencia filogeográficos estimados para las siete especies, claramente se observa que en el oeste de México han ocurrido una serie de cambios climáticos que han afectado la distribución de los bosques. La evidencia de estos eventos en los últimos 35.000 años permite pensar en cambios similares para un periodo mucho más antiguo que pudieron fragmentar los bosques secos del oeste de México. De hecho los mapas de vegetación potencial para el Pleistoceno en México, indican que el bosque seco del oeste mexicano estuvo interrumpido por bosque húmedo y bosque de coníferas [68, 69] a la altura del Eje Neovolcánico y en algunos puntos de Guerrero, Michoacán y Oaxaca que podrían relacionarse con las divisiones filogeográficas encontradas. Considerando mis datos y la información recabada sobre cambios en vegetación se podría plantear el sigueinte escenario hipotético. Las zonas montañosas cercanas la costa (y las tierras bajas aledañas) pudieron haber sido zonas de inestabilidad climática donde la vegetación cambió de bosque seco a otro tipo de vegetación mas asociada a humedad (*e.g.*, bosques mesofilos o selvas humedas) debido a incrementos de la precipitación y disminuciones de temperatura que pudieron haber disminuido los déficits de humedad asociados con un clima seco a través de una menor evotranspiración [109]. La vegetación más húmeda representa un ambiente en el que no se encuentran varias de las especies endémicas del bosque seco [31, 32], de modo que su ocurrencia histórica en la zona fragmentaría las distribuciones de las especies, disminuyendo el flujo génico entre poblaciones y generaría la diferenciación filogeográfica observada. Otros eventos como incrementos en el nivel del mar pudieron contribuir también a disminuir el área de las tierras bajas e interrumpir el flujo génico entre poblaciones. No obstante la ausencia de una congruencia completa entre las especies y los diferentes tiempos en que posiblemente se originó la estructura filogeográfica de cada una indican que la respuesta de cada especie fue idiosincrática y que la fragmentación de los bosques secos debió darse en diferentes momentos durante los últimos 500.000 años.

En este trabajo he mostrado evidencia de especiación *in situ* de *P. mexicanus* con respecto a su especie hermana *P. longirostris* de las selvas húmedas de México y Centro América [26]. Además, la existencia de zonas de diferenciación biogeográfica en o cerca a las zonas identificadas aquí como de disrupción filogeográfica sugiere que diferentes procesos, durante un periodo extenso, han tenido un papel en la diferenciación de la biota del oeste de México. No obstante las diferencias en el ADN no se relacionan completamente con diferencias fenotípicas entre poblaciones de dos de las especies [26, 27]. Los resultados de este trabajo también llevan a plantear la pregunta acerca del tipo de cambios ocurridos en la zona que promovieron diferenciación filogeográfica en especies que muestran cierto grado de tolerancia a modificaciones antrópicas del paisaje. Como indiqué esta disrupción podría seberse a la existencia de vegetación asociada a una mayor humedad. Evidencia paleopalinológica mas antigua que la que existe (e.g. 100, 000 años de antiguedad) podría validar mi propuesta. Finalmente, en otras regiones costeras tropicales que tienen una distribución mas o menos norte-sur, y que están bordeadas por cadenas montañosas, también se han encontrado patrones semejantes de estructura filogeográfica en varias especies [83, 101, 116-119]. Por lo tanto, mis resultados podrian hacer parte de un patrón mas general de diferenciacion intraespecífica en las biotas tropicales de zonas con una geografia singular.

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