UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

Estudio comparativo de la evolución vocal en avifaunas insulares

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

MARCO FABIO ORTIZ RAMÍREZ

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

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
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ÍNDICE

Resumen

Los cantos de las aves pueden actuar como una barrera reproductiva debido a su función en la atracción de pareja. Sin embargo, diversos factores como la morfología, las diferencias genéticas, el clima, el tipo de vegetación, los eventos de colonización y el aislamiento geográfico, entre otros pueden hacer que los cantos varíen entre poblaciones. Mi objetivo fue analizar cómo las diferencias genéticas, la morfología del pico, el tipo de hábitat y la historia biogeográfica podrían dar forma a los cantos en cuatro especies de aves paseriformes del Archipiélago de las Islas Tres Marías (TMA). Analicé si las diferencias en el canto de los pájaros están relacionadas con diferencias morfológicas o ecológicas (temperatura, precipitación y tipo de hábitat) entre TMA y el continente. También busqué evidencia de migración entre las islas y el continente comparando los tamaños de repertorio y el índice de fijación genética (FST). Además, estimé el espacio acústico que utilizan las cuatro especies entre islas y continente a partir de sus cantos y exploré si las diferencias en el espacio acústico se explican mejor por la morfología, las diferencias genéticas, las condiciones ambientales, el tipo de hábitat, el aislamiento geográfico o interacciones entre éstas variables. Descubrí que las características ecológicas están afectando las diferencias de los cantos de aves entre TMA y el continentales. Aparentemente, el hábitat afecta la transmisión de sonido directamente o indirectamente como resultado de diferencias morfológicas en los picos. Los índices de fijación genética (FST) e intercambio de sílabas sugieren un bajo flujo cultural y genético entre TMA y el continente. La evidencia genética sugiere que las poblaciones de TMA se aislaron durante miles de años. Por lo tanto, el aislamiento de las poblaciones en las islas es un factor importante en la divergencia del canto. Probablemente, una reducción en la diversidad biológica amplió el espacio acústico disponible para los colonizadores. De modo que, la combinación del tiempo transcurrido desde la colonización, el efecto fundador, las diferencias ecológicas, las bajas tasas de migración y probablemente una menor selección sexual, han favorecido la fijación de diferentes rasgos en las poblaciones de TMA que evolucionan independientemente del continente.

Palabras clave: Ventana acústica, Colonización, Aislamiento, Efecto fundador, Pleistoceno.

Abstract

Birdsongs can act as a reproductive barrier due to their function in mate attraction. However, several factors such as morphology, genetic differences, weather, vegetation type, colonization events and geographic isolation, among others, can cause birdsong variation between populations. My main goal is to analyze how genetic differences, bill morphology, habitat type and biogeographic history could shape the songs of four species of passerine birds in the Tres Marías Islands Archipelago (TMA). I analyzed whether the differences in birdsongs are related to morphological or ecological differences (temperature, precipitation and habitat type) between TMA and the continent. I also looked for evidence of migration between the islands and the continent comparing the repertoire sizes and the genetic fixation index (FST). In addition, I estimated the acoustic space used by four species between islands and mainland according to their songs and explored if differences in the acoustic space are best explained by morphology, genetic differences, environmental conditions, habitat type, geographic isolation or interactions between these variables. I discovered that ecological characteristics are affecting the differences in birdsong between TMA and mainland. Apparently, habitat affects sound transmission directly or indirectly as a result of bill morphological differences. The values of the genetic fixation index (FST) and the syllable exchange index suggest a low cultural and genetic flow between TMA and mainland. Genetic evidence suggests that TMA populations were isolated for thousands of years. Therefore, the isolation of TMA populations is also an important factor that contributed to the divergence of their songs. Probably, a reduction in biological diversity expanded the acoustic space available to colonizer's songs. So, the combination of the time since colonization event, the founder effect, the ecological differences, the low migration rates and probably a lower sexual selection, have favored the fixation of different traits in the TMA populations that evolve independently of the continent.

Key words: Acoustic window, Colonization, Isolation, Founder effect, Pleistocene.

Introducción general

Las diferencias en las características físicas que presentan las islas con respecto al continente como la temperatura, humedad y precipitación o las diferencias ecológicas como abundancia de alimento, refugios, predadores y competencia intra e interespecífica, aunadas al aislamiento geográfico, afectan en conjunto las diferencias morfológicas, acústicas y genéticas entre las poblaciones continentales e insulares (Weigelt et al. 2013). Particularmente en las islas de origen volcánico cuyas poblaciones frecuentemente son fundadas por colonizadores provenientes del continente (Thornton 2007), dichas diferencias son pequeñas en un principio y con el paso del tiempo y la reducción del flujo genético, las diferencias pueden llegar a ser tales como para considerarlas especies distintas (Weigelt et al. 2013). Cuando las diferencias entre las poblaciones son pequeñas, hablamos de microevolución, la cual se refiere a los cambios inherentes en las características de un grupo de organismos a través de generaciones (Kingsolver y Pfenning 2014). Estos cambios pueden ser resultado de eventos de colonización, mutaciones, selección natural y sexual, los cuales modifican los fenotipos en respuesta al entorno o bien, los fenotipos cambian por procesos estocásticos como la deriva génica (Clegg 2010; McPeek 2014). A pesar de que los procesos microevolutivos no son exclusivos de islas (Clegg 2010), a menudo, los cambios graduales (microevolutivos) se acumulan a lo largo del tiempo y dan paso a la macroevolución, que es definida como la evolución a nivel de especie (Futuyma y Kirkpatrick 2017).

Estudios previos han observado que en algunos organismos las poblaciones insulares han evolucionado a una tasa acelerada al compararlas contra poblaciones continentales e incluso entre otras islas (Losos y Ricklefs 2009). Particularmente en aves, el aislamiento geográfico de las poblaciones tiene una fuerte influencia en la formación de nuevas especies (Mayr 1942; Diamond 1977). Por ejemplo, si los individuos que colonizan una nueva isla se ven sujetos a nuevas presiones de selección esto podría acelerar el proceso de especiación (Andersen et al. 2018). Por el contrario, si la selección no es el factor que está modificando las diferencias entre las poblaciones, entonces éstas podrían ocurrir de manera azarosa por deriva génica (Aleixandre et al. 2013; Futuyma y Kirkpatrick 2017). Además, el número reducido de individuos que normalmente colonizan las islas favorece la fijación de mutaciones en la población y podría generar diferencias entre las poblaciones insulares y continentales (efecto fundador; Mayr 1954; Lynch y Baker 1986; James et al. 2016). Al final, estos mecanismos podrían generar cambios significativos en tiempos relativamente cortos entre las poblaciones de islas y el continente. La evidencia muestra que en aquellas islas cuyas condiciones ambientales difieren con respecto al continente, someten a los colonizadores a diferentes presiones de selección ecológica favoreciendo a aquellos individuos cuyas características les brinden una ventaja para subsistir en la isla (Grant 2017). Frecuentemente en las islas los recursos son más limitados que en el continente (Mühlenberg et al. 1977; Meiri 2007), por lo tanto, la competencia por alimento, defensa del territorio u obtención de parejas puede ser mayor y ocasionar que aquellas características (genéticas, morfológicas y/o conductuales) que aumentan sus probabilidades de subsistencia y reproducción sean diferentes de las que son favorecidas en el continente (Berglund et al. 1996; Grant 2017).

En el ámbito reproductivo y conductual de las aves, una de las principales conductas para atraer pareja es el canto, el cual, también es utilizado en otros contextos como defensa del territorio y reconocimiento de especies (Catchpole y Slater 2008). Un factor relevante en la formación de nuevas especies es la selección por parte de las hembras (Boughman 2016), que en ocasiones, promueve que las ornamentaciones morfológicas y conductuales que presentan los machos sean muy elaboradas. Por ejemplo, en las aves del paraíso en la isla de Nueva Guinea, se cree que los plumajes llamativos, las danzas de cortejo exuberantes y la gran variedad de cantos que presentan los machos son debidos a una fuerte presión de selección sexual sobre dichas características (Seddon et al. 2013; Boughman 2014; Webb et al. 2016). Por el contrario, en algunas islas se ha sugerido una relajación de la selección sexual para explicar la existencia de cantos menos complejos (menor diversidad de sílabas) en comparación con el continente (Searcy y Andersson 1986; Price 1998; Hamao y Ueda 2000; Hamao 2013). La cual, aparentemente se debe a una menor competencia entre machos como resultado de una menor abundancia de individuos (Goretskaia 2004; Garamszegi 2012).

Sin embargo, los cantos de las aves también se ven seriamente afectados por la forma y tamaño de los picos de las aves (Podos 2001; Huber y Podos 2006), así como por las diferencias en el tamaño corporal (Ryan y Brenowitz 1985; Podos et al. 2004). Ambas características limitan las frecuencias en que las aves emiten sus cantos (Huber y Podos 2006). Frecuentemente, en las poblaciones insulares los picos de las aves presentan diferencias en tamaño y forma con respecto a las poblaciones continentales u otras islas y se piensa que se debe a diferencias en su dieta por la escasez o disponibilidad de recursos alimenticios (Grant 1965). Por ello, es de esperarse que las diferencias morfológicas entre las poblaciones de islas y continente afecten la reproducción de forma directa, o bien de forma indirecta al modificar los cantos que emiten los machos.

Además, los cantos también están limitados por selección natural, vía transmisión del sonido en el ambiente (Endler 1992; Slabbekoorn y Smith 2002; Tobias et al. 2010). Dicha transmisión del sonido es afectada por las condiciones que presenta el entorno como son el tipo y densidad de la vegetación, la temperatura y la humedad del ambiente, favoreciendo o limitando la trasmisión de algunas señales acústicas (Morton 1975; Ryan y Brenowitz 1985; Wiley y Richards 1978, 1982). Weir et al. (2012) analizaron la importancia de factores ecológicos como el tipo de vegetación, la riqueza de especies y la presencia de insectos con alta actividad acústica, en la variación vocal de especies hermanas. Ellos encontraron que los patrones de divergencia en las frecuencias de los cantos de las aves tropicales están relacionados con las propiedades de transmisión del sonido y la competencia acústica. Sin embargo, Luzuriaga-Aveiga y Weir (2019) encontraron que a pesar que las diferencias ecológicas aceleran la divergencia acústica, no siempre aceleran la tasa de especiación.

La hipótesis conocida como “sensory drive” fue propuesta por Endler (1992) para explicar cómo el ambiente local afecta las características físicas de los sistemas de comunicación (emisión y detección de señales), de modo que, si hay una diferencia en las condiciones ambientales, entonces habrá cambios en los mecanismos de comunicación que favorezcan una transmisión de forma más eficiente. Si las condiciones ambientales entre las islas y el continente son diferentes, entonces los colonizadores podrían desarrollar diferencias con respecto al continente y con el paso del tiempo podría haber especiación (Boughman 2002). Por ejemplo, Tobias et al. (2010) compararon 17 especie de aves con sus respectivas especies hermanas, mismas que habitan diferentes tipos de hábitat en el Amazonas, y encontraron evidencia de que los cantos de las aves evolucionaron con relación a las propiedades de transmisión del sonido en el hábitat y no como resultado de divergencia genética, masa corporal o tamaño del pico. La hipótesis “sensory drive” ha sido corroborada principalmente en señales visuales. Sin embargo, en señales auditivas muchas veces los resultados no han sido favorables (Cummings y Endler 2018). Lo cual sugiere que otros factores sean responsables de la evolución acústica.

En general, la consecuencia de la divergencia vocal en la formación de nuevas especies es evidente debido a su relevancia en la discriminación intra e interespecífica (Catchpole y Slater 2008; Wilkins et al. 2013). Sin embargo, aún es incierto si la divergencia acústica entre poblaciones es más relevante como una barrera reproductiva precigótica que promueve la especiación o bien, si tiene una función más relevante como un mecanismo de aislamiento reproductivo que refuerza la discriminación entre miembros de diferentes especies (Wilkins et al. 2013). En ocasiones, las modificaciones en caracteres relacionados con la alimentación podrían afectar el canto y ser promotores de la divergencia. Por lo tanto, una forma de elucidar si los cantos promueven la especiación en las islas o la refuerzan es analizando la manera en que los cantos se ven afectados por las características que influyen en su producción, transmisión y herencia.

Como hemos visto existen varias causas por las cuales se producen diferencias vocales entre poblaciones. Por lo tanto, la divergencia acústica de las poblaciones de aves insulares y continentales puede ser resultado de una mezcla de diferentes factores. Si bien, en algunos casos ciertos factores actúan de forma severa en las poblaciones generando divergencia entre las poblaciones y especies (Mason et al. 2017), existen otros factores que pueden ser ligeramente apreciables o incluso pasar desapercibidos al ser diluidos por el flujo génico o cultural (Lynch y Baker 1986). Por esta razón, estudiar el efecto que tienen distintos factores sobre las poblaciones insulares es de gran relevancia para comprender de mejor manera cómo evolucionan las aves, tanto por el aislamiento geográfico como por la interacción de las características relacionadas con la explotación de recursos, supervivencia y reproducción (Grant y Grant 2017), y en consecuencia afectando la tasa de especiación (Rabosky 2016). El presente trabajo tiene como objetivo general analizar la variación acústica de las poblaciones de cuatro especies de aves del archipiélago de las Islas Tres Marías con respecto a las poblaciones cercanas en el continente contrastando la variación genética, la morfología, el tipo de hábitat y el clima (temperatura y precipitación). El trabajo consta de tres capítulos: En el primer capítulo reviso la manera en que caracteres genéticos, morfológicos y vocales se ven afectados por el aislamiento geográfico. En el segundo capítulo analicé a detalle el efecto del aislamiento geográfico en la divergencia genética de cuatro especies de aves paseriformes entre el oeste de México y las Islas Tres Marías, considerando los eventos históricos que han favorecido la colonización de las islas. En el tercer capítulo exploré la relación que tienen los factores genéticos, ecológicos (temperatura, humedad y tipos de vegetación), y morfológicos (tamaño del pico y tamaño corporal) con las diferencias entre poblaciones insulares y continentales en los cantos de cuatro especies de aves paseriformes. Finalmente, resalto las conclusiones más importantes de la tesis y ofrezco nuevas hipótesis que podrían explicar cómo han evolucionado los cantos de las aves en las Islas Tres Marías.

CAPÍTULO I

EFECTO DEL AISLAMIENTO GEOGRÁFICO EN LA EVOLUCIÓN DE LOS RASGOS GENÉTICOS, MORFOLÓGICOS Y BIOACÚSTICOS DE AVES INSULARES Y SU RELEVANCIA PARA LA ESPECIACIÓN

Efecto del aislamiento geográfico en la evolución de los rasgos genéticos, morfológicos y bioacústicos de aves insulares y su relevancia para la especiación

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Resumen

En islas oceánicas las poblaciones de aves frecuentemente divergen de sus contrapartes continentales en características genéticas, morfológicas y acústicas a través de la disminución del flujo genético y cultural. Sin embargo, las diferencias en factores ecológicos como la alimentación, la temperatura o el tipo de vegetación, promueven cambios en las características morfológicas, particularmente en el tamaño corporal y el tamaño y forma del pico. Las diferencias morfológicas producen variación en la frecuencia, ritmo y composición de notas o sílabas del canto. Además, en las islas continentales, el efecto fundador puede ocasionar que exista una menor variedad de sílabas en comparación con las poblaciones continentales. Durante el Pleistoceno los cambios climáticos aislaron y reconectaron varias de las islas oceánicas cercanas al continente, afectando las características genéticas, morfológicas y conductuales. Esto pudo favorecer la aparición de nuevas sílabas y cantos, y afectar el reconocimiento específico lo que favorece una reproducción diferencial que a largo plazo puede generar diferenciación entre las poblaciones o incluso especiación.

Palabras clave: Aislamiento geográfico, Vocalizaciones, Alopatría, Variación geográfica, Pleistoceno, Cambios climáticos.

Abstract

In oceanic islands, bird populations often diverge from their continental counterparts in genetic, morphological, and acoustic characteristics through the decrease in genetic and cultural flow. However, differences in ecological factors such as food resources, temperature, or vegetation type, promote changes in morphological characteristics, particularly in body and bill size and shape. Morphological differences produce variation in the frequency, rhythm, and syllable composition of bird songs. In addition, founder effect may cause a smaller variety of syllables in island vs. continental populations. Pleistocene climatic changes isolated and reconnected several oceanic islands near mainland, affecting genetic, morphological, and behavioral characteristics, promoting the appearance of new syllables and songs, and affecting species recognition. Because bird songs are crucial for mate attraction, this could produce differential reproduction that in long-term can generate differentiation between populations or even speciation.

Key words: Geographic isolation, Vocalizations, Allopatry, Geographic variation. Pleistocene, Climate changes.

INTRODUCCIÓN

Uno de los principales objetivos de la biología evolutiva es entender los procesos que promueven la diferenciación entre las poblaciones de los organismos, y la manera en que influyen en la formación de nuevas especies (Spurgin et al., 2014). Entre ellos, el aislamiento geográfico (alopatría) es muy relevante en la formación de nuevas especies de aves (Coyne y Price, 2000; Turelli et al., 2001). Por ello, las islas oceánicas son consideradas como laboratorios naturales para el estudio de la evolución (Losos y Ricklefs, 2009). Esto se debe a que tienen límites bien definidos por los mares y generalmente son de tamaño pequeño, lo que permite catalogar su flora y fauna con mayor facilidad que en el continente (Emerson, 2002; Losos y Ricklefs, 2009). Frecuentemente, el flujo génico entre islas y continente es reducido por las barreras oceánicas (Emerson, 2002). Sin embargo, a pesar de su tamaño relativamente pequeño, las islas pueden poseer una gran diversidad de hábitats con diferencias significativas en relación al continente (Emerson, 2002). Esto genera diferentes presiones de selección, mismas que promueven diferencias morfológicas, conductuales y genéticas entre los individuos y como resultado de la reducción del flujo genético y del tiempo de aislamiento, las poblaciones insulares pueden formar nuevas especies (Futuyma y Kirkpatrick, 2017). Por esta razón las islas frecuentemente se encuentran habitadas por una gran cantidad de especies endémicas que, por su historia de colonización, tienen especies hermanas en las áreas continentales cercanas a la isla (Cowie y Holland, 2006; Oliveros y Moyle, 2010; Sly et al., 2011).

La biota presente en las islas es resultado de diferentes factores. Por ejemplo, el origen de la isla (oceánica o continental), su tamaño y fisiografía, la manera en que se dispersan los organismos, y la distancia de la isla al continente, entre otros (Mac Arthur y Wilson, 1967; van der Geer et al., 2010). Debido a su origen volcánico, las islas oceánicas debieron ser colonizadas por los organismos a través de eventos de dispersión, lo que implica que los individuos colonizadores arribaron provenientes de una fuente aportadora, como lo es el continente o incluso otra isla en el caso de los archipiélagos (Emerson, 2002; Fabre et al., 2012; Feo et al., 2014). En ocasiones, las poblaciones insulares son fundadas por un número reducido de individuos, y como consecuencia, pueden presentar bajos niveles de diversidad genética, lo cual se conoce como efecto fundador (Hedrick, 2014). Con el paso del tiempo, la baja diversidad genética producida por el efecto fundador y la fijación de los alelos en la población, pueden generar divergencia entre la población fuente e insular (Campagna et al., 2012) e incluso, si el aislamiento geográfico reduce severamente el flujo génico entre las poblaciones, puede conllevar a especiación (Price, 2008; Campagna et al., 2012; Feo et al., 2014).

La vagilidad es la capacidad de los organismos de moverse a través de su entorno (Levin 2009), por lo tanto, tiene un papel importante en el aislamiento geográfico de las poblaciones, de manera que afecta directamente el flujo genético y por ende la diferenciación entre poblaciones (Mayr y Diamond, 2001; Emerson, 2002; Kodandaramaiah, 2009; Deiner et al., 2011). En varios estudios se ha observado que colonizar nuevas áreas con diferentes condiciones ambientales, habitadas por distintos depredadores, y diferente disponibilidad de alimento, puede generar variación entre las poblaciones (Orr y Smith, 1998; Juan et al., 2000; Emerson, 2002).

En este trabajo reviso como la variación en los cantos de las aves se relaciona con la divergencia en otros caracteres como la genética, la morfología y el aislamiento geográfico. Además, abordo la similitud que existe entre los procesos que afectan la variación genética y la variación vocal como la mutación, la deriva génica y la selección, particularmente en poblaciones insulares. Las cuales, frecuentemente han colonizado en un momento dado y comúnmente presentan un efecto fundador que con el paso del tiempo ha generado divergencias en diferentes rasgos de las especies. Finalmente, discuto la manera en la que la variación acústica, causada por los distintos factores, está estrechamente relacionada con la formación de barreras reproductivas, mismas que promueven la formación de nuevas especies.

Importancia evolutiva de la variación geográfica en los cantos de las aves

Los biólogos evolutivos han estado interesados por mucho tiempo en entender cómo y por qué los organismos varían geográficamente (Podos y Warren, 2007). Incluso, entre los cantos de las aves podemos encontrar variación geográfica (Payne, 1986). El canto en las aves es una señal que sirve para la comunicación (Catchpole y Slater, 2008), y por lo tanto son vitales en la atracción de pareja y reproducción, por ello están sujetos a una fuerte presión de selección (Catchpole, 2000). En los cantos de las aves podemos observar variación microgeográfica y variación macrogeográfica. La microvariación se refiere a los dialectos que se definen como variantes del canto compartidas por los miembros de una población con un límite bien definido enfatizando la evolución cultural, siendo únicamente patrones conductuales y no genéticamente definidos (Mundinger, 1982). La macrovariación se refiere a la variación a escala regional sobre todo en el repertorio de sílabas y enfatiza los procesos evolutivos (Mundinger, 1982).

Los cantos de las aves son una herramienta útil en la identificación de relaciones filogenéticas debido a que parte de ellos está determinada genéticamente (Payne, 1986). Sin embargo, en las aves oscinas (Orden: Passeriformes) parte del canto es aprendido, ya sea a través de los padres o de individuos vecinos (Cavalli-Sforza et al., 1982). Esto sugiere que en algunas especies existe la posibilidad de que individuos cercanamente relacionados presenten cantos muy diferentes y viceversa (Olofsson y Servedio, 2008; Ortiz-Ramírez et al., 2016). Por ejemplo, en el Gorrión corona blanca (*Zonotrichia leucophrys pugetensis*) Soha et al. (2004) encontraron una clara diferencia vocal entre poblaciones, sin embargo, genéticamente no encontraron diferencias significativas. Los dialectos ocurren en aves que aprenden sus cantos y se definen como variación en los cantos de un sitio a otro e incluso entre individuos de una misma población, con o sin diferenciación genética (Podos y Warren, 2007; Catchpole y Slater, 2008). Esto no quiere decir que no se pueda encontrar un patrón en los caracteres vocales. En los Reyezuelos (género *Regulus*) Päckert et al. (2003) observaron que los cantos poseen una señal filogenética. La cual puede deberse a que la característica de aprender los cantos está determinada genéticamente (Payne, 1986). Entre las especies que aprenden sus cantos, la familia Mimidae se caracteriza por presentar una gran variedad de cantos (incluso de miles de cantos) como en los Cuitlacoches (género *Toxostoma*;

Boughey y Thompson, 1981). Otras especies como el Centzontle norteño (*Mimus polyglottos*) incorporan en sus repertorios de cantos sonidos de otras especies con las que cohabitan (Price y Yuan, 2011). Por lo que el aprendizaje de los cantos de las aves puede ser un problema si se desea emplearlos como caracteres en el estudio de sus relaciones filogenéticas.

Price y Lanyon (2002) mostraron que a pesar del aprendizaje y de lo complicado que pueden llegar a ser los cantos de las aves, sí es posible esclarecer las relaciones filogenéticas de los taxones mediante caracteres vocales. Ellos compararon la filogenia de un grupo de Oropéndolas obtenida mediante caracteres vocales contra otra obtenida con caracteres genéticos. En ambas filogenias obtuvieron prácticamente las mismas relaciones filogenéticas. Esto se debe a que los cantos tienen un papel fundamental para las aves en la atracción de pareja (Marler, 1960). Por lo tanto, pueden servir como barrera reproductiva reduciendo el flujo genético, y a lo largo del tiempo generar divergencias (Catchpole y Slater, 2008).

Factores que modifican la divergencia genética y vocal

De manera similar a lo que ocurre con los genes, los cantos de las aves están sujetos a factores como innovación (mutación), deriva cultural (deriva génica), migración (flujo génico) y selección (Lynch, 1996). Cuando en una población existen variaciones genéticas hablamos de diversidad genética, de manera análoga las variaciones vocales representan la diversidad vocal. Cuando ocurre un evento de colonización hacia las islas (o una nueva área), dependiendo de la efectividad de la barrera, sólo una parte de esa diversidad (genética o vocal) se hace presente en las nuevas áreas debido al efecto fundador (Baker et al., 2006). Por esta razón, es común encontrar diferencias entre los cantos de las poblaciones insulares y continentales. Aunque en ocasiones esto no ocurre o bien se restituyen a corto plazo (Gardner et al., 2005; Morinay et al., 2013). En general, los cantos que emiten las poblaciones en las islas son de mayor duración en comparación con sus contrapartes continentales, pero lo hacen presentando una menor variedad de sílabas, es decir que, en la elaboración de su canto repiten varias veces algunas de ellas (Baptista y Johnson, 1982; Naugler y Smith, 1991; Baker et al., 2006; Xing et al., 2013). Sin embargo, también existe la invención de sílabas completamente nuevas o variantes de una sílaba preexistente, mismas que después de un tiempo pueden fijarse en las poblaciones (Lynch, 1996). Esto depende del tamaño de la población, de la presión de selección a la que se ven sujetas, y de la tasa de migración que podría disminuir su proporción en la población (Lynch, 1989).

La deriva cultural, es una variación en las sílabas que es causada por los errores al aprender el canto de un individuo a otro y se van fijando poco a poco en la población, esto puede generar diferencias vocales entre las poblaciones si el tiempo es suficiente para que se acumulen suficientes y se pierda el reconocimiento conespecífico (Lynch y Baker, 1994; Grant y Grant, 1996; Lynch, 1996; Podos y Warren, 2007). En general, la tasa de mutación vocal puede ser muy rápida en comparación con la tasa de mutación genética (Xing et al., 2013). Por lo tanto, el flujo de individuos entre poblaciones afecta la divergencia vocal. Cabe señalar que a diferencia de los genes (en los organismos con reproducción sexual), los cantos y sílabas pueden pasar de una población a otra sin que los individuos migrantes dejen descendencia, esto es debido a que los individuos locales pueden incorporar sílabas y cantos aprendidos de los individuos migrantes a sus propios repertorios únicamente por aprendizaje (Cavalli-Sforza et al., 1982). Esto se conoce como transferencia cultural horizontal y transferencia cultural oblicua, de lo contrario cuando la transferencia cultural se da de padres a hijos se conoce como transferencia cultural vertical (Cavalli-Sforza et al., 1982).

La selección por parte del entorno hacia las vocalizaciones se da en la transmisión del sonido. Ya que las características ambientales como la temperatura, la humedad y el tipo de vegetación, están relacionadas con las frecuencias en que los organismos emiten sus vocalizaciones, favoreciendo a aquellas frecuencias o tipos de sílabas que mejor se transmitan en el lugar que habitan (Morton 1975; Endler, 1992; Slabbekoorn et al., 2002; Slabbekoorn y Smith, 2002; Slabbekoorn y Smith, 2002). Frecuentemente, las condiciones ambientales entre islas y continente son similares, aunque no necesariamente son iguales. Por lo tanto, los cantos de un individuo de una población quizás no sean favorecidos en otra población. Algunos estudios han observado que los individuos ajustan sus cantos dependiendo de las condiciones ambientales (Slabbekoorn y Smith, 2002). Si los cantos son aprendidos de una generación a otra, y las poblaciones habitan en lugares con condiciones ambientales diferentes, es probable que con el paso del tiempo se pierdan aquellas silabas desfavorecidas en unas condiciones y que se fijen las favorecidas, produciendo divergencias vocales entre poblaciones (Baker, 2006). O bien, en el caso de los archipiélagos vayan disminuyendo gradualmente la similitud de sus cantos conforme las poblaciones estén más distantes con respecto al continente (Lachlan et al., 2013). Como consecuencia, esto podría reducir el reconocimiento conespecífico y actuarían como una barrera reproductiva (Wright y Dahlin 2018).

Los eventos de colonización podrían potencialmente generar diferencias en el tamaño del repertorio de sílabas presente en la nueva población, debido a que al ser fundadas por un número reducido de individuos, representan una submuestra de la variación total de la población fuente (Lynch y Baker, 1986; Baker y Jenkins, 1987; Baker et al., 2001). Sin embargo, en islas cercanas al continente o a la población fuente, una mayor magnitud del flujo genético y/o cultural (migración) podría disminuir la variación y reducir la tasa de divergencia entre las poblaciones a tal grado que incluso podría homogeneizarlas (Baker y Jenkins, 1987; Lynch y Baker, 1994).

Consecuencias del aislamiento geográfico en la divergencia genética y conductual.

Uno de los principales efectos que tiene el aislamiento geográfico sobre las poblaciones es la divergencia genética (Futuyma y Kirkpatrick, 2017). Una manera de estudiarlo es mediante la filogeografía, la cual integra los principios y procesos que gobiernan la distribución geográfica de los linajes, especialmente dentro de taxones cercanamente relacionados (Avise, 2000). De este modo la información geográfica y genética permiten inferir la historia evolutiva del taxón y brindar información de los procesos que dieron origen a la divergencia (Deiner et al., 2011; Sly et al., 2011). En ausencia de flujo génico o cuando éste es muy bajo, las poblaciones alopátricas divergen como resultado de la fijación de los diferentes alelos ancestrales o mutaciones (Futuyma y Kirkpatrick, 2017). Eventualmente, algunos de los alelos fijados podrían afectar la ecología, etología, fisiología o biología reproductiva de los linajes (Harrison, 2014).

Para colonizar exitosamente una isla primero deben existir las condiciones favorables para la subsistencia del taxón, o que éste sea capaz de adaptarse a las nuevas condiciones y no extinguirse (Orr y Smith, 1998; Juan et al., 2000). Además, la probabilidad de colonización de un taxón hacia una isla es proporcional a la distancia y su capacidad de dispersión (Mac Arthur y Wilson, 1967; Kodandaramaiah, 2009). Si el taxón en cuestión tiene una amplia adaptabilidad y buena vagilidad entonces el flujo de individuos a través de la barrera geográfica será mayor y potencialmente mantendría el flujo génico (Kodandaramaiah, 2009; Feder et al., 2014). Por el contrario, si el taxón tiene gran vagilidad pero poca adaptabilidad sólo podrá colonizar las nuevas áreas cuando las condiciones le sean favorables y por lo tanto, el flujo génico será menor (Kodandaramaiah, 2009; Feder et al., 2014). En algunos casos la efectividad de la barrera también puede variar a lo largo del tiempo, por ejemplo, los cambios en el nivel del mar durante las glaciaciones pudieron favorecer el flujo génico entre poblaciones durante los periodos glaciares y volver a reducirse durante los interglaciares (Upchurch y Hunn, 2002; Barber y Klicka, 2010). De modo que las características ecológicas, la topografía y la cercanía de las islas al continente, también son relevantes para entender los procesos que ocurren en las poblaciones insulares.

Actualmente, podemos encontrar diversos ejemplos de aves cuyas poblaciones insulares muestran cierto grado de diferenciación genética o incluso presentan elementos suficientes para ser consideradas especies diferentes (Coyne y Price, 2000; Lohman et al., 2010; Sánchez-González et al., 2015; Hosner et al., 2018). En las islas Malvinas Campagna et al. (2012) analizaron las diferencias genéticas de nueve especies de aves con respecto al continente. Seis de ellas compartieron haplotipos entre sus respectivas poblaciones insulares y continentales; dos presentaron haplotipos únicos en las poblaciones insulares con un paso mutacional con respecto a los del continente; y sólo una especie, (*Troglodytes cobbi*), presentó una gran divergencia entre islas y continente. Es probable que la variación en la diferenciación genética se deba a que las especies experimentaron diferentes niveles de migración, diferentes tamaños efectivos poblacionales o a que colonizaron las islas en diferentes tiempos (Campagna et al., 2012). En otro estudio Fabre et al., (2012) encontró que los mosqueros del paraíso (género

Terpsiphone), los cuales colonizaron el sureste de Asia, África y varias islas del océano Índico, diversificaron en varias de las nuevas áreas que colonizaron e incluso desarrollaron diferencias no sólo genéticas sino también en la coloración del plumaje.

En general, el factor importante en la divergencia de los linajes no es simplemente el que las poblaciones estén separadas, sino qué tan efectiva es la barrera para reducir el flujo génico. El hecho de que los individuos puedan desplazarse de una población a otra, no implica que se reproduzcan en la población a la que arribaron (Randler et al., 2012; Ronce, 2014; Schluter, 2014). Esto sugiere la existencia de un mecanismo de emparejamiento selectivo que constituye una barrera precigótica, como los cantos u otras características físicas o conductuales (Price, 2008; Wilkins et al., 2013; Ritchie, 2016), o bien la existencia de barreras postcigóticas que impiden la formación del gameto o la viabilidad del mismo por incompatibilidad genética (Price, 2008; Ritchie, 2016). En el caso de los Barbudos de Asia (Krishnan y Tamma 2016) encontraron que la divergencia en morfología y cantos es crucial para la coexistencia de especies cercanamente relacionadas. Otro ejemplo es el de los Bulbules de las Filipinas, donde Oliveros y Moyle (2010) encontraron evidencia de al menos siete eventos de colonización hacia las islas que aparentemente ocurrieron simultáneamente y concluyeron que la diversidad de especies presentes en éstas islas no se debe únicamente a la colonización sino también a especiación *in situ* (Oliveros y Moyle, 2010). Esto sugiere la existencia de una reproducción selectiva. Por su parte, Lohman et al. (2010) analizaron los patrones filogenéticos de siete especies de aves consideradas de amplia distribución incluyendo poblaciones en las islas Filipinas. Ellos encontraron que todas eran altamente divergentes con respecto a sus poblaciones continentales, presentando monofilia recíproca y sugirieren que las poblaciones insulares deben ser consideradas como especies diferentes. En muchas ocasiones, estas divergencias genéticas están acompañadas de divergencias en otros caracteres como los morfológicos, conductuales y ecológicos.

Relación entre la variación morfológica y los cantos de las aves

En las islas comúnmente existen diferencias ecológicas y ambientales que han favorecido cambios drásticos en la morfología de las aves, sobre todo en el tamaño y forma del pico, estas características del pico junto con las condiciones ambientales están estrechamente relacionadas con los cantos de las aves (Grant y Grant, 2006). En los pinzones de las Galápagos se observó que el tipo de cantos que emite cada una de las especies, varía de acuerdo al tamaño y forma del pico, haciendo que las aves con picos cortos y menos robustos tienden a emitir más sílabas por unidad de tiempo en comparación con aves de picos largos y robustos (Podos, 2001). A pesar de los distintos factores ecológicos que afectan los tipos de cantos en las aves (Ryan y Brenowitz, 1985; Endler, 1992, Slabbekoorn y Smith, 2002), las vocalizaciones pueden contribuir en los procesos de especiación (MacDougall-Shackleton y MacDougall-Shackleton, 2001; Grant y Grant, 2006; Olofsson y Servedio, 2008) y poseer información filogenética (McCracken y Sheldon, 1997).

Otro rasgo morfológico que varía en las islas con relación al continente es el tamaño corporal (Clegg y Owens, 2002; Losos y Ricklefs, 2009). En aves, el tamaño corporal está determinado en gran medida por la temperatura del ambiente (Olson et al., 2009). Wallschläger (1980) observó que las aves de mayor tamaño corporal emitían cantos más graves y mientras menor era el tamaño, los cantos eran más agudos. Estas diferencias pueden ser seleccionadas por parte de las hembras (Boughman, 2016; Walsh et al., 2018). En algunas poblaciones reproductivamente compatibles, las características conductuales, como los cantos, forman una barrera precigótica evitando el flujo génico y favoreciendo la divergencia de taxones cercanamente relacionados (Wilkins et al., 2013). En las islas oceánicas el efecto fundador es muy relevante debido a que generalmente representan una submuestra de la variación genética, morfológica y conductual (Frankham, 1997). Algunos autores sugieren que, en las islas debido a que comúnmente los tamaños poblacionales son menores existe una relajación de la selección sexual, esto permite que aquellas variantes que en la población continental no habrían sido favorecidas prevalezcan en las poblaciones insulares (Hamao, 2013).

Importancia del aislamiento geográfico y cambios climáticos en la evolución de aves en islas

Trabajos recientes en islas han demostrado la importancia del aislamiento geográfico en la etapa inicial de la formación de especies (Grant et al., 2000), así como los efectos de los eventos fortuitos históricos y factores determinísticos en la evolución de especies en islas (Losos y Ricklefs, 2009). En islas cercanas al continente las barreras geográficas pudieron ser inconsistentes durante ciertas épocas (Wang et al., 2016). Por ejemplo, las oscilaciones climáticas que ocurrieron durante el Pleistoceno tuvieron un efecto dramático en la evolución de las especies, debido a los cambios que propiciaron en la distribución geográfica y en la demografía de diversas especies (Hewitt, 1996; Hewitt, 2000; Nadachowska-Brzyska et al., 2015). En el caso de las islas, durante los cambios climáticos del Pleistoceno ocurrieron cambios drásticos en el nivel del mar de alrededor de 100 m por debajo del nivel actual (Flint, 1947; Yokoyama et al., 2000; Hofreiter y Stewart, 2009; Ramos-Fregonezi et al., 2015). Esto pudo haber generado periodos de aislamiento poblacionales y subsecuentes reconexiones o simplemente una reducción en la efectividad de la barrera geográfica. Además de que existieron cambios considerables en las temperaturas ambientales (Hofreiter y Stewart, 2009). La distribución de la diversidad genética contemporánea se debe en gran medida a cómo respondieron los organismos a esos cambios climáticos en una escala geológica (Hewitt, 1996; Kerdelhue et al., 2009). Sin embargo, el efecto de las glaciaciones en la evolución de las diferentes especies ha sido diferencial (Klicka y Zink, 1999; Lovette, 2005; Zhao et al., 2012). Para algunas especies sus poblaciones continentales pudieron desplazarse en busca de las condiciones ambientales que les fueron favorables mediante la migración (Milá et al., 2006). Por el contrario, la situación fue drásticamente diferente para las poblaciones insulares, que en algunos casos presentaron cambios altitudinales o latitudinales (Kerdelhue et al., 2009). Para aquellas especies cuyas capacidades de dispersión no les permitieron desplazarse en busca de condiciones favorables, los individuos tuvieron que adaptarse a las condiciones, se extinguieron o disminuyeron drásticamente sus poblaciones (Kerdelhue et al., 2009). Si consideramos que los tamaños efectivos poblacionales pequeños pudieron resultar en una disminución de la diversidad genética, entonces la evolución en las islas pudo haber ocurrido a una tasa mucho mayor en comparación con el continente al permitir fijar las diferencias mucho más rápido (Kerdelhue et al., 2009).

En general, las oscilaciones climáticas del Pleistoceno crearon periodos de contracción y expansión de las poblaciones causando en muchos casos divergencias genéticas, morfológicas y/o vocales (Hewitt, 1996; Avise y Walker, 1998; Qu et al., 2010; Zhao et al., 2012). Por esta razón, estimar los tiempos de divergencia a partir de las secuencias genéticas utilizando un "reloj molecular" abre la posibilidad de analizar los diferentes factores que pudieron haber generado la divergencia otros caracteres (Heads, 2012). Si dos o más especies co-distribuidas (y que no están emparentadas) presentan el mismo patrón de divergencia pero a diferentes profundidades en el árbol filogenético, podría ser evidencia de que evolucionaron a diferentes tiempos con historias biogeográficas independientes (Joseph y Omland, 2009). Sin embargo, una explicación alternativa es que la diferenciación haya ocurrido al mismo tiempo pero con tamaños de poblaciones ancestrales diferentes (Edwards y Beerli, 2000; Joseph y Omland, 2009). En las poblaciones con menor número de individuos el sorteo de linajes podría ser más rápido que en una población de mayor número de individuos, y por lo tanto interpretarse de manera errónea como una divergencia a diferentes tiempos, debido a que las poblaciones más grandes requieren más tiempo para el sorteo de linajes (Joseph y Omland, 2009).

En las islas de Filipinas Sánchez-González et al. (2015) encontraron que las divergencias en tres taxones ocurrieron durante los cambios climáticos del Pleistoceno que aislaron sus poblaciones. Sin embargo, unos ocurrieron a principios del Pleistoceno y otros al final. La evidencia sugiere que en el sureste asiático, durante el último periodo glacial, la región conocida como la región de la Sonda (Indonesia y Malasia) formó una península con una vegetación de sabanas (Bird et al., 2005). En la actualidad ésta zona está fragmentada en diferentes islas: Sumatra, Java y Borneo. Probablemente, los periodos glaciares e interglaciares aislaban y reconectaban de manera cíclica las poblaciones restringiendo el flujo génico y cultural. De este modo se favorecieron algunas características morfológicas dependiendo de las condiciones ambientales. Evidentemente esto ha afectado a una gran cantidad de taxones y ha favorecido la divergencia de los mismos que como resultado a generado la diversidad que existe en la actualidad en varias partes del mundo y sobre todo en islas (Avise y Walker, 1998; Hewitt, 2000; Weir y Schluter, 2004; Grant y Grant, 2006). Para discernir si algunos linajes cuyos caracteres no son tan evidentes se han empleado diferentes fuentes de información como so los genes, la ecología, la morfología y sus vocalizaciones de manera conjunta y se ha concluido que pueden distinguirse linajes que han evolucionado independiente y que merecen ser considerados como especies (Cadena y Cuervo, 2009).

Conclusiones

Las islas han favorecido el aislamiento geográfico de muchos taxones, lo cual en muchas veces ha generado divergencias debido al bajo o nulo flujo génico entre poblaciones. En ocasiones las condiciones ecológicas han promovido diferencias morfológicas en las poblaciones insulares en características relacionadas al canto como son el tamaño corporal y el tamaño y forma del pico. Además, en islas oceánicas, el efecto fundador en ocasiones reduce la variedad de sílabas y cantos en relación al continente. Las diferencias en los cantos pueden tener consecuencias en el reconocimiento específico y actuar como barrera reproductiva. En las islas existen una gran cantidad de endemismos crípticos que hace falta estudiar más a detalle. En años recientes el uso de diversos caracteres para definir el estatus taxonómico de diversas aves ha aumentado, entre ellos los caracteres vocales cada vez están tomando mayor relevancia. Si la biología se enfoca en entender y analizar los procesos que han dado origen a la diversidad que vemos en la actualidad, hacerlo utilizando la mayor cantidad de evidencia posible es fundamental para entender mejor la evolución de los seres vivos y la historia biogeográfica de cada uno de ellos.

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CAPÍTULO II

FILOGEOGRAFÍA COMPARADA DE LAS ISLAS TRES MARÍAS

(ARTÍCULO DE REQUISITO)

Ortiz-Ramírez, Marco Fabio, Luis A. Sánchez-González, Gabriela Castellanos-Morales, Juan Francisco Ornelas, y Adolfo G. Navarro-Sigüenza. 2018. Concerted Pleistocene dispersal and genetic differentiation in passerine birds from the Tres Marías Archipelago, Mexico. *The Auk* 135(3): 716–732. https://doi.org/10.1642/auk-17-190.1.

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RESEARCH ARTICLE

Concerted Pleistocene dispersal and genetic differentiation in passerine birds from the Tres Marías Archipelago, Mexico

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ABSTRACT

Studies in evolutionary biology have commonly been focused on insular systems because of their natural geographic isolation and relatively simpler biotas. Using mitochondrial DNA sequences of 4 passerine bird species distributed in the Tres Marías Archipelago (TMA) and the nearby mainland of western Mexico—*Cardinalis cardinalis*, *Turdus rufopalliatus*, *Vireo hypochryseus*, and *Icterus pustulatus*—we determined interspecific and intraspecific phylogenetic relationships between insular and mainland populations, conducted insular age-based time calibration for the estimation of divergence times, and used Bayesian analyses to examine the colonization history of islands. Specifically, we tested whether the study species from the TMA share the same colonization history since the emergence of the islands ~120 kya, taking advantage of the reduced isolation due to sea-level fluctuations during the Pleistocene, or whether there were independent colonization events. We also looked for evidence in the genetic structure of the island populations that would support the idea of colonization by a small number of individuals. Phylogenetic relationships consistently recovered lineage divergence between the TMA and mainland populations, with strong support in 3 of the 4 species. Our estimates for the sea level and coastline of the west coast of Mexico during the Pleistocene showed that the distance between the TMA and the mainland was ~25 km. We tested several island colonization scenarios according to the phylogenetic relationships, haplotype networks, divergence time estimates, historical demography, and different glaciation dates. The most supported scenario of colonization of the TMA suggests that a single event occurred ~120 kya when the islands emerged, which is highly concordant with geological evidence, and simultaneously affected the 4 species.

Keywords: divergence, glaciations, island colonization, isolation, phylogeography

Dispersión conjunta durante el Pleistoceno y diferenciación genética de aves paseriformes del Archipiélago de las Tres Marías, México

RESUMEN

Debido a su aislamiento geográfico natural y sus biotas relativamente más simples, los estudios de biología evolutiva comúnmente se han centrado en sistemas insulares. En esta contribución, nosotros usamos secuencias de ADN mitocondrial (mtDNA) de cuatro especies de aves paserinas distribuidas en el Archipiélago de las Tres Marías (ATM) y el territorio continental cercano en el occidente de México, y determinamos las relaciones filogenéticas inter e intraespecíficas entre las poblaciones insulares y continentales, estimamos el tiempo de divergencia en las poblaciones insulares basadas en calibraciones de la edad de las islas, y usamos análisis Bayesianos para probar la historia de colonización de las islas. Específicamente, probamos si esas cuatro especies de aves paserinas del ATM comparten la misma historia de colonización desde que emergieron las islas hace alrededor de 120 mil años, aprovechando la reducción del aislamiento debido a las fluctuaciones del nivel del mar durante el Pleistoceno, o si fueron eventos de colonización independientes. También investigamos si existe evidencia en la estructura genética de las poblaciones de las islas que respalde la idea de la colonización por un número pequeño de individuos. Las relaciones filogenéticas recuperaron consistentemente la divergencia entre los linajes del ATM y del continente, con un fuerte apoyo en tres de las cuatro especies. Nuestras estimaciones para el nivel del mar y la línea de costa del oeste de México durante el Pleistoceno mostraron que la distancia entre las islas y el continente era de ~25 km. Por lo tanto, probamos varios escenarios de colonización de las islas de acuerdo a las relaciones filogenéticas, las redes de haplotipos, las estimaciones del tiempo de divergencia, la demografía histórica y las diferentes fechas de glaciaciones. El escenario más apoyado de colonización del ATM sugiere que fue un solo evento, el cual ocurrió aproximadamente hace 120 mil años cuando surgieron las islas, y que afectó simultáneamente a las cuatro especies de aves paseriformes, lo que concuerda en gran medida con la evidencia geológica.

Palabras clave: aislamiento, colonización de islas, divergencia, filogeografía, glaciaciones

INTRODUCTION

Understanding the evolutionary processes of island bird populations has been a central theme in avian biology (Rodrigues et al. 2013). Islands have been a primary focus of evolutionary biologists, who have used them as natural experimental areas (Losos and Ricklefs 2009, Aleixandre et al. 2013) to study features such as isolation, relatively small size, distinctive boundaries, and simplified biotas, which have shaped the evolution of highly distinctive biotic assemblages (Losos and Ricklefs 2009).

The biogeographic origins of insular biotas have also long attracted scientific attention, both from a static view that insular species richness has remained highly stable over time, and from a more appealing and dynamic view in which insular species richness results from a dynamic equilibrium between opposing rates of colonization and extinction (MacArthur and Wilson 1963, 1967). From an evolutionary perspective, there are 2 main processes that may lead to a distinctive insular biota: (1) vicariance, mostly on land-bridged islands; and (2) dispersal to oceanic islands that emerged de novo as a result of volcanic activity (Mayer 2013). Specifically for oceanic islands, limited or interrupted gene flow between the newly established population and the source population, as well as highly reduced dispersal opportunities, are significant conditions for evolutionary divergence (Leisler and Winkler 2015). Time provided, island colonization and subsequent diversification can lead to speciation, increasing species richness on islands.

Island colonization can also occur through dispersal, a process that, when it occurs simultaneously in lineages that share space and time, may influence their evolutionary trajectories, resulting in highly similar patterns of divergence and colonization that can be approached through phylogenetic reconstruction methods (Mantooth and Riddle 2011). Islands are also of particular interest because climatically based cyclical changes in the ice sheets' extension during the Quaternary promoted global shifts in temperature, precipitation, and sea levels (reaching $\sim$100 m below present levels), leading to periods in which many oceanic islands close to continents experienced reduced geographic isolation and thus increasing opportunities for colonization and posterior isolation (Yokoyama et al. 2000, Hofreiter and Stewart 2009, Chan et al. 2014). Alternate periods of isolation and reconnection may, in turn, enhance population diversification (Avise and Walker 1998, Avise et al. 1998, Klicka and Zink 1999). In addition, Plio-Pleistocene climatic fluctuations shaped species' distributions at a global scale (Hewitt 1996, 2000, Dolman and Joseph 2012). Lastly, oceanic islands could have experienced both extinctions and recolonizations, even without climate fluctuations (Kvist et al. 2005).

A long-standing issue in evolutionary biology is whether geographic isolation is a prerequisite for the evolution of reproductive isolation, or whether the latter can evolve in sympatry (Coyne and Price 2000). Evidence supporting one of these conditions may come from comparisons of range size between sister taxa, which suggest that speciation may be attributable either to the isolation of small populations (the "isolation-by-distance" model; e.g., Irwin et al. 2005) or to founder effects (Barraclough and Nee 2001). In this context, analysis of genetic markers has provided a powerful approach for testing these alternatives, because results can be interpreted in terms of evolutionary processes such as colonization and isolation (Lawson Handley et al. 2011). In addition, species-level phylogenies of insular lineages can provide information on speciation rates, as well as on the accumulation of lineages through time (Barraclough and Nee 2001, Warren et al. 2003).

A careful use of oceanic-island age estimates for time tree calibration has the theoretical advantage of providing maximum age constraints for relatively shallow divergences; fossils, in comparison, tend to provide minimum age boundaries and are therefore useful mostly for deeper clades (Lovette 2004, Ho and Phillips 2009, Hawlitschek et al. 2017). However, these bounds must also be chosen carefully (Ho and Phillips 2009, Ho et al. 2015), because molecular studies have provided ambiguous evidence suggesting either younger or older ages (especially for island endemics) for insular taxa in comparison to the age of the island they inhabit (Heads 2011, Hawlitschek et al. 2017).

Studies of intraspecific mitochondrial DNA (mtDNA) from bird populations in archipelagos have shed light on patterns of gene flow and on biogeography (Kirchman and Franklin 2007). Examining phylogenetic patterns of different codistributed species may reveal common processes resulting in highly similar evolutionary patterns (Hickerson et al. 2006, Kirchman and Franklin 2007, Burbrink and Castoe 2009, Gutiérrez-García and Vázquez-Domínguez 2011). Two kinds of methods have frequently been applied to the analysis of probable colonization routes: (1) methods based on long-term observations of the involved taxa (direct methods) and (2) indirect methods based on the analysis of patterns produced by population genetics (Estoup and Guillemaud 2010). To analyze colonization pathways, the approximate Bayesian computation (ABC) method is frequently used to compare competing scenarios from which biogeographic inferences can be drawn (Beaumont et al. 2002, Cornuet et al. 2014), whereas the hierarchical ABC (HABC) is a more powerful technique for testing simultaneous divergence of multiple taxon pairs (Huang et al. 2011). On the other hand, the study of mainland and island populations of a species within a given region is highly significant for the understanding of the evolutionary dynamics affecting populations in habitats that have been assembled through different processes (Jensen et al. 2013), which also may have important implications in regard to conservation issues for taxa and populations (see Lohman et al. 2010).

The volcanic islands of the Tres Marías Archipelago (hereafter TMA), located offshore of western Mexico, are an ideal system for studies of colonization and divergence processes because of 2 significant features that may lead to opportunities for colonization: isolation and divergence. First, María Madre Island, the oldest one, apparently emerged above sea level only 120 kya (McCloy et al. 1988), thus setting a maximum date for testing the hypotheses of either concerted or separated dispersal for the avifauna. Second, during the Pleistocene, the TMA was closer to the mainland (24–32 km) than it is today (~95 km), because of sea-level lowering since then (Zweifel 1960). Of the 191 bird species recorded in the archipelago, 61 breed there and the other 130 comprise the terrestrial bird community (Grant and Cowan 1964, Grant 1965, Hahn et al. 2012). Most terrestrial bird species in the TMA have closely related populations distributed along the tropical deciduous and sub-deciduous forest in the nearby continental areas (Stager 1957) and differ from their mainland counterparts both phenotypically and genotypically, leading to the recognition of endemic subspecies for most of these resident forms (Grant 1965, Phillips 1981, Howell and Webb 1995, Peterson and Navarro-Sigüenza 2000, Cortés-Rodríguez et al. 2008, Smith et al. 2011, Arbeláez-Cortés et al. 2014b, Montaño-Rendón et al. 2015). These observations suggest that the TMA is an important region for bird diversification in western Mexico. In spite of this, the TMA avifauna has barely been studied and its biogeography is unclear (Stager 1957). Most bird species in the archipelago are thought to be derived from nearby mainland relatives. However, distinctive distributional patterns in mainland populations of a few bird species (see Stager 1957) suggest that other alternatives may be possible. In addition, it is not known whether insular populations diverged from those on the mainland as a consequence of a single biogeographic event or whether the TMA has been colonized several times. In the present study, we used mtDNA sequences of 4 passerine bird species distributed in the TMA and western Mexico to determine phylogenetic relationships between insular and mainland populations, estimate divergence times, and test for a shared colonization history. Specifically, we asked whether the 4 species of birds from the TMA share the same colonization history since the emergence of the islands around 120 kya (McCloy et al. 1988), taking advantage of the reduced isolation due to sea-level fluctuations during the Pleistocene, or whether there were independent colonization events. We also investigated the genetic structure of the island populations for evidence suggesting colonization by a small number of individuals.

METHODS

Study Area

The TMA is located 132 km west of San Blas, Nayarit, Mexico (21.77°N–21.25°N, 106.69°W–106.19°W; Figure 1). The archipelago consists of 4 islands—María Cleofas, María Magdalena, María Madre, and San Juanito—with elevations ranging from sea level to 650 m (María Madre). The islands are covered mainly by tropical deciduous and sub-deciduous forest mixed with thorn scrub, mangroves, and cacti. The rainy season occurs from June to December (Grant 1965, Hahn et al. 2012).

Taxon Sampling

In designing our study, we selected 4 passerine species that are codistributed along the Pacific slope of western Mexico and the TMA. These birds can be considered representatives of the taxonomic diversity (4 different families) and ecological diversity (mainly feeding habits and habitat use) of the passerine landbird community as a whole in the tropical dry forest of the islands and mainland, including granivores, frugivores, and insectivores; ground and foliage foragers; and abundances ranging from ecologically restricted to ubiquitous. The study species are also those for which we have the most complete geographic coverage for the islands and mainland in terms of genetic data, both in available GenBank sequences and in tissue samples for sequencing; in addition, previous molecular studies have shown that both the TMA and mainland populations of all these species are genetically differentiated from each other (see below). We used mitochondrial sequences ND2 (nicotine amide dehydrogenase 2) and cyt *b* (cytochrome *b*) deposited in GenBank and newly sequenced for this project for the following taxa: the Northern Cardinal (*Cardinalis cardinalis*; Smith et al. 2011), a widely distributed species ranging from southern Canada and the eastern United States to northern Guatemala and Belize; the Rufous-backed Robin (*Turdus rufopalliatus*; Montaño-Rendón et al. 2015) and the Golden Vireo (*Vireo*

FIGURE 1. Map of the Pacific coast of Mexico and the Tres Marías Archipelago. Dotted line depicts the shoreline during the Pleistocene glaciations with sea level 100 m below the current level (Yokoyama et al. 2000), as estimated using General Bathymetric Chart of the Oceans data (2014 2D; http://www.gebco.net). Solid line depicts the current area above sea level and country boundaries. Abbreviations: TMA = Tres Marías Archipelago; SON = Sonora; CHIH = Chihuahua; SIN = Sinaloa; BCS = Baja California Sur; DGO = Durango; ZAC = Zacatecas; NAY = Nayarit; JAL = Jalisco; MICH = Michoacán; GRO = Guerrero; OAX = Oaxaca.

hypochryseus; Arbeláez-Cortés et al. 2014b), both endemic to western Mexico and the TMA; and the Streak-backed Oriole (*Icterus pustulatus*, from which 31 sequences were newly generated and one was obtained from GenBank; Omland et al. 1999), which ranges from northwestern Mexico (NWM) to northern Central America. In total, we obtained 183 samples (Supplemental Material Appendix A).

To elucidate which mainland populations are more closely related to TMA populations and whether they constitute potential sources for TMA colonization, we defined populations according to the clades obtained in the phylogenetic analyses (see below). However, given that *C. cardinalis* is the only species with distribution in NWM and Baja California Sur (BCS) for which phylogenetic evidence suggests that both populations belong to the same clade (Smith et al. 2011, Smith and Klicka 2013), analyses were done recognizing 2 groups following a geographic arrangement: one included populations in western Mexico and the other included the populations in the southern Baja California Peninsula in BCS. This arbitrary separation allowed us to identify population sources for colonization of the TMA.

Phylogenetics and Divergence Times

We analyzed mtDNA sequence data using a Bayesian inference method in BEAST 1.7 (Drummond et al. 2012). We obtained best substitution models based on Akaike's Information Criterion (AIC) for each gene using jModeltest 2 (Darriba et al. 2012). We tested the fit of our data to either a strict clock model or a relaxed clock model by using the stepping-stone sampling method (Kumar and Filipski 2001, Battistuzzi et al. 2011, Ronquist et al. 2011) in MrBayes 3.2 (Ronquist and Huelsenbeck 2003, Ronquist et al. 2012). We partitioned sequences in 3 codon positions and set the speciation Yule Process tree prior (Gernhard 2008) with a strict molecular clock prior (according to our clock test results; see below). Although we acknowledge that there is not a universal mtDNA clock for birds (García-Moreno 2004, Lovette 2004), we decided to use a mitochondrial rate of 1.23×10^{-2} substitutions site^{-1} lineage^{-1} myr^{-1} for both genes (Shields and Wilson 1987, Fleischer et al. 1998, Lovette 2004, Weir and Schluter 2008, Smith et al. 2011), because most of the calibrations for birds cluster around this value (García-Moreno 2004, Lovette 2004). We ran the analyses for 600 million

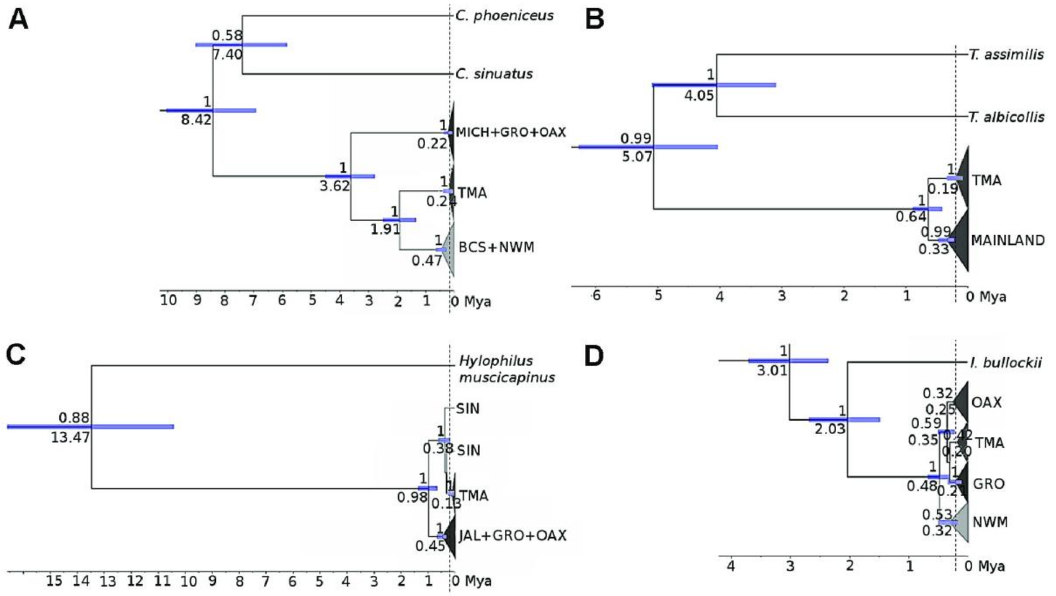

FIGURE 2. Phylogenetic relationships of each study species: (**A**) *Cardinalis cardinalis*, (**B**) *Turdus rufopalliatus*, (**C**) *Vireo hypochryseus*, and (**D**) *Icterus pustulatus*. Scale = mya; blue bars indicate 95% HPD interval for node ages; numbers above bars are posterior probability of the node; numbers below bars are estimated age of the node (time to most recent common ancestor); dashed lines mark 120 kya. Abbreviations: TMA = Tres Marías Archipelago; BCS = Baja California Sur; GRO = Guerrero; OAX = Oaxaca; JAL = Jalisco; MICH = Michoacán; SIN = Sinaloa; NWM = Sonora, Sinaloa, Nayarit, and part of Jalisco; MAINLAND = all continental populations.

generations, sampling every 6,000 generations, and assessed stationarity by comparing trace plots of the –ln*L* values (ESS values >200) in Tracer 1.5 (Rambaut and Drummond 2007). We discarded the first 25% of trees as burn-in; all remaining trees were summarized in a 50% majority rule consensus with a posterior probability (PP) $\geq$0.5 using TreeAnnotator 1.9 (Drummond et al. 2012). Node ages are presented as 95% highest posterior density (HPD).

Genetic Structure

Because intraspecific gene evolution cannot always be represented by a bifurcating tree (Posada and Crandall 2001), we assessed genetic relationships of the mtDNA haplotypes by constructing a median-joining haplotype network (Bandelt et al. 1999) using Network 4.6 (http://www.fluxus.engineering.com), which may be a more appropriate representation of haplotype relationships at the population level (Burbrink and Castoe 2009).

To analyze genetic diversity, we grouped samples for each species according to the clades we obtained in the phylogenetic analyses (Figure 2). We then estimated the following parameters using Arlequin 3.5 (Excoffier and Lischer 2010): nucleotide diversity (π), haplotype diversity (Hd), and Watterson's θ as a measure of DNA polymorphism (Watterson 1975). We assessed genetic structure for each species, using an analysis of molecular variance (AMOVA; Excoffier et al. 1992), in which *F* statistics were calculated among and within clades obtained in the trees. We ran a total of 10,000 nonparametric permutations to test the significance of the AMOVA (Excoffier et al. 1992). In our F_{ST} interpretation, following Hartl and Clark (1997), values 0–0.05 denote low, 0.05–0.15 moderate, 0.15–0.25 high, and >0.25 very high genetic differentiation.

We calculated historical demographic changes through parameters that may suggest changes in population size by estimating departures from neutrality (Fu 1997). The following analyses were estimated in Arlequin 3.5 (Excoffier and Lischer 2010) and DNAsp 5 (Librado and Rozas 2009), assessing significance by coalescence with 10,000 permutations: (1) Tajima's *D*, which tests for selective neutrality (Tajima 1989a, 1989b); (2) Fu and Li's *F*, which tests whether populations are evolving according to a neutral Wright-Fisher model (Fu 1997); and (3) the R_2 parameter (Ramos-Onsins and Rozas 2002), which has been demonstrated to be more robust than Fu and Li's *F*-test for detecting population growth with small sample sizes (Ramos-Onsins and Rozas 2002, Burbrink and Castoe 2009). In addition, we plotted mismatch distributions, which test the null hypothesis of population growth under 2 scenarios: constant population growth and a birth/death rate (Slatkin and Hudson 1991, Rogers and Harpending 1992, Burbrink and Castoe 2009). Unimodal and positively skewed mismatch distributions are frequently observed in populations that undergo a recent range expansion; multimodal (including bimodal) distributions are observed in populations that undergo a diminishing or structured population size; finally, a ragged (multimodal) distribution is observed in populations within widespread lineages (Rogers and Harpending 1992, Burbrink and Castoe 2009). However, a multimodal distribution is also indicative of either migration between populations or genetically subdivided populations or has undergone historical reduction (Marjoram and Donnelly 1994, Bertorelle and Slatkin 1995, Ray et al. 2003). We determined the validity of the estimated demographic model by using the sum of squared deviations (SSD; Excoffier and Schneider 1999, Schneider and Excoffier 1999); significant SSD values are frequently interpreted as a signature of no population expansion (Excoffier and Schneider 1999). We also estimated a raggedness index for the mismatch distributions (Harpending 1994): values are high (>0.05) for multimodal distributions of populations; low values (<0.05) are obtained for unimodal distributions typically observed in populations that have experienced sudden demographic expansion (Harpending 1994, Morando et al. 2008). We validated the raggedness index by comparison of probabilities of obtaining high values (P_{Ragg}) under the hypothesis of population growth (Morando et al. 2008).

Tests of Simultaneous Diversification

We tested whether simultaneous genetic differentiation occurred between islands and mainland populations of the 4 species by performing an HABC analysis (see above) using msBayes (Hickerson et al. 2007, 2014). This analysis evaluates scenarios of simultaneous divergence vs. nonsimultaneous divergence in pairs of populations by estimating hyperparameters that define the variability in divergence times of populations sharing space and time, while allowing for variation in demographic parameters (Burbrink and Castoe 2009). We ran 1×10^6 simulations under a scenario of multiple divergence times with the prior for τ set to 0.120, corresponding to the date of the TMA emergence (McCloy et al. 1988), and assuming no migration between populations. The upper θ value was estimated as part of the analyses. We set the prior for the maximum number of divergence events (ψ) to 4, which corresponds to the maximum numbers of taxa if each species has a different colonization time. A value of $\Omega = 0$ is expected for a set of species pairs that share a unique divergence event (Hickerson et al. 2006).

Estimation of Colonization Routes

To investigate the possible existence of a shorter distance or even a land bridge between islands and mainland during the sea-level lowering in the Pleistocene (Zweifel 1960), which may have provided a colonization pathway for different taxa, we obtained bathymetric data from the General Bathymetric Chart of the Oceans (2014 2D; http://www.gebco.net), which is a grid file for geographic information systems (GIS) with a spatial resolution of 30 arc seconds, with negative values for bathymetric depths and positive values for topographic heights. We transformed data into elevation curves. Then data were reclassified in intervals of 50 m to estimate the coastline limits with a sea-level scenario 100 m below the present level, using the option "level curves" of the extraction tool of the Raster menu in QGIS 2.16 (http://www.qgis.org). We selected the 100 m high line to represent the shoreline in the raster basemap of the world (TM World Borders 0.3; http://thematicmapping.org), which corresponds to the estimated sea level during the Pleistocene climatic changes (Yokoyama et al. 2000). Distance between TMA and mainland shoreline was estimated in QGIS.

We tested hypotheses for different colonization scenarios for each species, depending on the number of populations, phylogenetic relationships, the structure of haplotype networks, and the dates of glacial periods (which may have affected the closeness of mainland to islands through the lowering of sea level) that occurred within the confidence intervals obtained in divergence time analyses for each species (see Supplemental Material Appendix B). Although all divergence times among all species occurred during the Pleistocene, confidence intervals were slightly different; thus, scenarios were different for each species. Therefore, to analyze the existence of a shared biogeographic history, we tested a general scenario for all species, in which islands were colonized by the closest mainland population, NWM, ~120 kya. We focused our analyses on this date because evidence suggests that islands emerged in this period (McCloy et al. 1988), but we tested other glacial dates for each species (e.g., 10 kya, which corresponds to the end of the Pleistocene; Supplemental Material Appendix B). Given that molecular sequences may allow drawing of inferences on routes for natural range expansion (Estoup and Guillemaud 2010), we used DIYABC 2.10 (Cornuet et al. 2014) because it better estimates routes of colonization than methods that do not consider genealogical information (see Cornuet et al. 2014). We ran DIYABC following Bertorelle et al.'s (2010) recommendations to assess for the appropriate priors. Populations were defined according to phylogenetic results. We estimated effective population sizes from θ values for each lineage; times to most recent common ancestors were obtained from the divergence time estimations; and the substitution rate was set to 1.23×10^{-2} substitutions site^{-1} lineage^{-1} myr^{-1} according to the "2%

TABLE 1. Marginal likelihood estimates (using stepping-stone method) testing for strict vs. relaxed molecular clock for sequence evolution in the study species.

Species	Relaxed clock	Strict clock
Cardinalis cardinalis	−5,129.25	−4,942.71
Turdus rufopalliatus	−10,765.78	−10,397.25
Vireo hypochryseus	−4,764.28	−4,621.79
Icterus pustulatus	−2,856.14	−2,853.52

rule" of avian divergence (Lovette 2004, Weir and Schluter 2008, Smith et al. 2011). We selected summary statistics to generate data simulations that contained information for our interest: the number of unique haplotypes and segregating sites, Tajima's *D* (for 1-sample summary statistics), and pairwise F_{ST} values (for 2-sample summary statistics). Then, for both model selection and checking, we followed recommendations for data simulations in Bertorelle et al. (2010).

RESULTS

Phylogenetic Relationships and Divergence Times between TMA and Mainland Bird Populations

We obtained 1,041 base pairs for ND2 sequences for 61 individuals of *C. cardinalis*, 55 individuals of *T. rufopalliatus*, and 34 individuals of *V. hypochryseus*; and 527 base pairs for 15 individuals of *I. pustulatus*. For cyt *b*, we were able to obtain only a partial fragment (~500 base pairs) of 22 individuals of *C. cardinalis*, 32 of *I. pustulatus*, 54 of *T. rufopalliatus*, and 11 of *V. hypochryseus*. Given these results, we analyzed *C. cardinalis* and *V. hypochryseus* with ND2 sequences only. The final concatenated dataset consisted of 61 sequences for *C. cardinalis* (all from GenBank); 56 for *T. rufopalliatus* (45 from GenBank and 11 newly sequenced for this project, from which 1 sample has only ND2 sequence and 2 samples have only cyt *b* sequences); 34 for *V. hypochryseus* (all from GenBank); and 32 sequences for *I. pustulatus*, most of them newly generated (one from GenBank; Supplemental Material Appendix A). All of our clocklike tests best supported a strict clock (Table 1).

Phylogenetic analyses consistently recovered TMA and mainland populations as reciprocally monophyletic groups. For *I. pustulatus* only, population relationships showed differences, in that TMA populations were recovered as sister to a mainland group including GRO and OAX (Figure 2). All estimates of divergence times between TMA and mainland populations in the 4 species dated back to the Pleistocene: 1.91 mya (95% HPD interval: 2.49–1.35 mya) for *C. cardinalis*; 0.64 mya (95% HPD interval: 0.89–0.42 mya) for *T. rufopalliatus*; 0.38 mya (95% HPD interval: 0.66–0.20 mya) for *V. hypochryseus*; and 0.35 mya (95% HPD interval: 0.51–0.22 mya) for *I. pustulatus* (Figure 2).

Haplotype Networks and Genetic Structure

Because all of our trees showed geographic structure between the TMA and mainland populations in the 4 species, we grouped populations according to the phylogenetic relationships to construct haplotype networks (for population names, abbreviations, and groups, see Figures 2 and 3). The number of unique haplotypes (Hap) found in each population is shown in Table 2. There were 29 mutational steps between TMA and mainland populations for *C. cardinalis* (Figure 3A). We observed 12 mutational changes for *T. rufopalliatus* between TMA and mainland populations from NWM, GRO, and OAX (Figure 3B). For *V. hypochryseus*, 2 samples from Sinaloa grouped closer to the TMA population (5 mutational changes) than to other mainland populations (Figure 3C). For *I. pustulatus*, there were 2 mutational changes between TMA and mainland populations; however, 1 sample grouped within the haplogroup from NWM. Haplotypes from Guerrero, Oaxaca, and Jalisco populations showed 2–4 mutational changes between them (Figure 3D). With the exception of the haplotype network for *V. hypochryseus*, all species showed or suggested a star-like pattern for haplotypes included in NWM populations.

In general, we obtained high values of haplotype diversity ($h > 0.5$) for both TMA and mainland populations in *C. cardinalis*, *T. rufopalliatus*, and *I. pustulatus*, but not for *V. hypochryseus*, in which all samples from the TMA shared the same haplotype (Table 2). Most mainland populations showed high haplotype diversity values except in the following populations: MICH+GRO+OAX for *C. cardinalis*; NWM and MICH+GRO+OAX for *T. rufopalliatus*; and GRO for *I. pustulatus* (Table 2); on the other hand, all populations in the 4 species showed low levels of nucleotide diversity ($\pi < 0.5\%$; Table 2).

Demographic History and Genetic Differentiation

Tajima's *D* values were not significant for any population, except for BCS and NWM populations of *C. cardinalis*. Fu and Li's *F* was negative and significant only for the MICH+GRO+OAX group of *C. cardinalis*, as well as for mainland *V. hypochryseus* (Table 2). Results of the R_2 index for historical demography among populations suggested demographic expansion only for BCS and NWM populations of *C. cardinalis* and the mainland population of *V. hypochryseus* (Table 2). Mismatch distributions and SSD estimates suggested demographic expansions for most of the populations (Table 2 and Figure S5). For *V. hypochryseus*, we were only able to estimate mainland population parameters because all TMA samples shared the same haplotype, and for Sinaloa we had only 2 samples (Table 2).

Genetic differentiation (F_{ST}) values between mainland and TMA were high (>0.25) for all species (according to

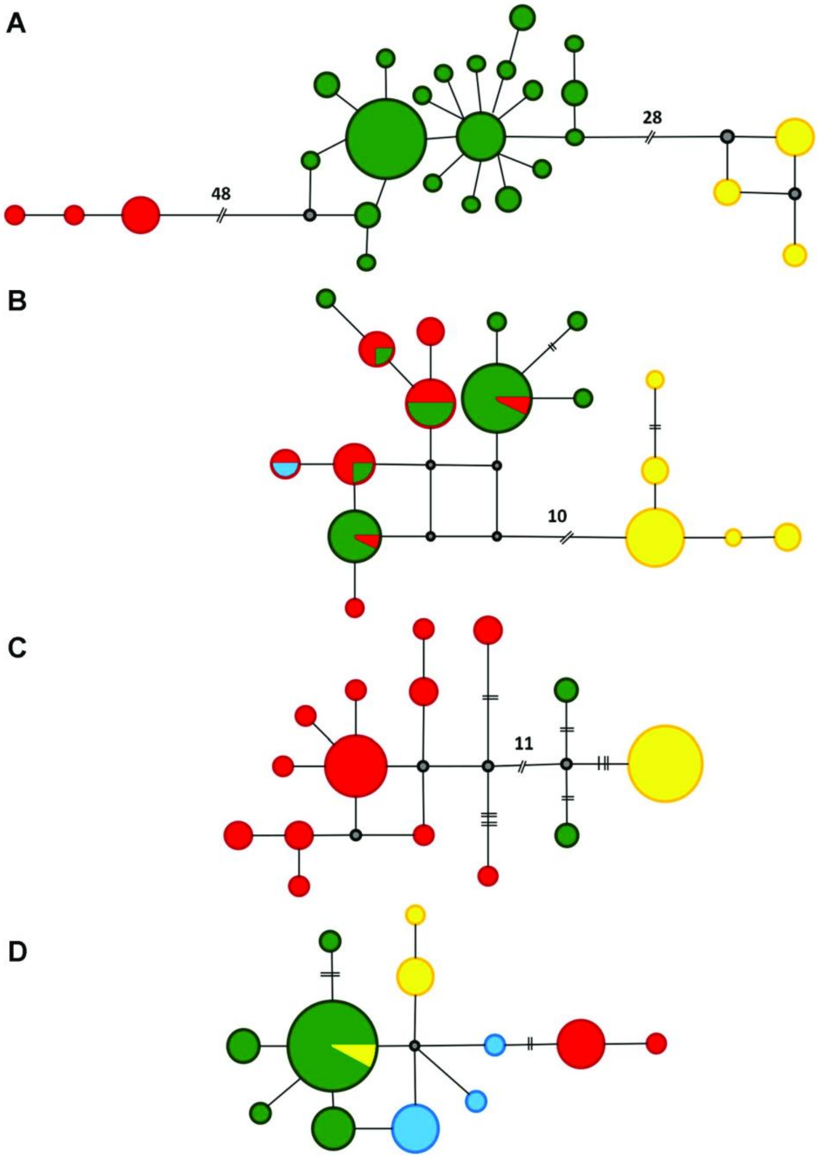

FIGURE 3. Haplotype networks obtained by MJ (Median-Joining) algorithm. (**A**) *Cardinalis cardinalis*: yellow = TMA, green = BCS+NWM, red = MICH+GRO+OAX. (**B**) *Turdus rufopalliatus*: yellow = TMA, green = NWM, red = MICH+GRO, blue = Oaxaca. (**C**) *Vireo hypochryseus*: yellow = TMA, green = SIN, red = mainland populations except Sinaloa. (**D**) *Icterus pustulatus*: yellow = TMA, green = NWM, red = GRO, blue = OAX (population abbreviations are defined in the text and in captions of Figures 1 and 2). Lines without numbers represent one mutation; each perpendicular line depicts one mutational change; numbers above diagonal parallel lines represent the number of mutational changes in that segment. Gray circles represent hypothetical or unsampled haplotypes.

TABLE 2. Genetic diversity and historical demography estimates between mainland and Tres Marías Archipelago populations and among all populations for each species. Populations are grouped according to phylogenetic results.

Taxon	Population	*n*	Hap	H_d	π	θ_π	*S*	*D* (*P*)	*F* (*P*)	SSD (*P*)	RI (*P*)	R_2 (*P*)
Cardinalis cardinalis	TMA	6	3	0.73	0.002	1.80	4	0.15 (0.62)	0.83 (0.67)	**0.11 (0.12)**	**0.35 (0.34)**	0.23 (0.42)
	MAINLAND Population	55	23	0.87	0.015	14.34	69	−0.17 (0.50)	0.22 (0.59)	**0.23 (0.08)**	**0.02 (0.64)**	0.10 (0.10)
	MICH+GRO +OAX	8	3	0.46	0.001	0.68	2	−0.45 (0.33)	−**12.74 (0.001)**	**0.01 (0.88)**	**0.13 (0.12)**	0.20 (0.13)
	BCS	17	12	0.92	0.002	2.41	14	−**1.60 (0.05)**	−**22.40 (0.001)**	0.02 (0.03)	0.09 (0.02)	**0.07 (0.001)**
	NWM	30	13	0.68	0.002	1.42	14	−**1.99 (0.01)**	−**27.89 (0.001)**	**0.02 (0.34)**	**0.09 (0.36)**	**0.05 (0.001)**
Turdus rufopalliatus	TMA	12	3	0.53	0.001	1.45	2	−0.45 (0.39)	−3.04 (0.11)	**0.002 (0.81)**	**0.03 (0.88)**	0.18 (0.32)
	MAINLAND Population	44	6	0.69	0.002	2.82	5	−0.06 (0.36)	−0.08 (0.48)	**0.03 (0.18)**	**0.07 (0.42)**	0.11 (0.33)
	NWM	30	5	0.40	0.001	1.50	1	−0.07 (0.41)	−0.07 (0.22)	0.02 (0.54)	0.13 (0.35)	0.13 (0.35)
	MICH+GRO +OAX	14	4	0.39	0.001	2.46	3	−0.42 (0.38)	−2.35 (0.06)	0.01 (0.28)	0.17 (0.16)	0.15 (0.28)
Vireo hypochryseus	TMA	9	1	0.00	0.000	0.00	0	0.00 (1.00)	NA	0.00 (0.001)	NA	NA
	MAINLAND Population	25	14	0.89	0.005	4.55	29	−1.21 (0.09)	**-4.65 (0.01)**	**0.001 (0.95)**	0.02 (0.05)	0.07 (0.01)
	SIN	2	2	1.00	0.004	4.00	4	0.00 (1.00)	1.39 (0.47)	0.00 (0.00)	2.00 (1.00)	0.50 (1.00)
	Mainland not SIN	23	12	0.87	0.003	2.87	16	−1.21 (0.08)	−**26.43 (0.00)**	**0.001 (0.96)**	0.01 (0.001)	0.08 (0.03)
Icterus pustulatus	TMA	5	3	0.70	0.001	2.00	4	−1.12 (0.06)	0.64 (0.62)	**0.09 (0.52)**	**0.29 (0.44)**	0.25 (0.49)
	MAINLAND Population	27	9	0.85	0.004	4.43	17	0.01 (0.58)	0.42 (0.63)	**0.02 (0.41)**	**0.05 (0.19)**	**0.09 (0.21)**
	NWM	16	4	0.66	0.001	1.57	5	0.15 (0.58)	0. 80 (0.68)	**0.03 (0.51)**	**0.11 (0.52)**	0.11 (0.12)
	GRO	5	2	0.40	0.001	0.80	2	−0.97 (0.10)	1.04 (0.59)	0.17 (0.00)	**0.68 (0.89)**	0.40 (0.80)
	OAX	6	3	0.60	0.002	2.73	7	−0.63 (0.31)	1.62 (0.78)	**0.18 (0.03)**	**0.35 (0.76)**	0.190 (0.24)

Notes: *n* = sample size. *P* values are in parentheses; significant *P* values ($\alpha = 0.05$, and $\alpha = 0.5$ for raggedness) are in bold. Numbers in bold depict population expansion. Abbreviations: MAINLAND = all mainland populations included; TMA = Tres Marías Islands; BCS = Baja California Sur; GRO = Guerrero; MICH = Michoacán; OAX = Oaxaca; SIN = Sinaloa; NWM = Sonora, Chihuahua, Sinaloa, Nayarit, and/or Jalisco; Hap = unique haplotype number; H_d = haplotype diversity; π = nucleotide diversity; S = segregating sites; *D* = Tajima's *D*; *F* = Fu and Li's *F*; RI = raggedness index; SSD = sum of squared deviations; R_2 = Ramos-Onsins and Rozas R_2 parameter.

TABLE 3. Pairwise fixation index (F_{ST}) among populations of each study species.

Species	Population	TMA	NWM	BCS	MAINLAND	MICH+GRO+OAX	GRO+OAX	SIN	GRO	OAX
Cardinalis cardinalis	TMA	–			NA		NA	NA	NA	NA
	NWM	**0.95**	–		NA		NA	NA	NA	NA
	BCS	**0.93**	**0.11**	–	NA		NA	NA	NA	NA
	MICH+GRO+OAX	**0.98**	**0.97**	**0.96**	NA	–	NA	NA	NA	NA
Turdus rufopalliatus	TMA	–		NA	NA	NA		NA	NA	NA
	NWM	**0.89**	–	NA	NA	NA		NA	NA	NA
	MICH+GRO+OAX	**0.85**	**0.47**	NA	NA	–	NA	NA	NA	NA
Vireo hypochryseus	TMA	–		NA		NA	NA		NA	NA
	SIN	**0.90**	NA	NA	**0.78**	NA	NA	–	NA	NA
	MAINLAND	**0.86**	NA	NA	–	NA	NA	NA	NA	NA
Icterus pustulatus	TMA	–		NA	NA	NA	NA	NA		
	NWM	**0.61**	–	NA	NA	NA	NA	NA		
	GRO	0.84	**0.84**	NA	NA	NA	NA	NA	–	
	OAX	**0.47**	**0.57**	NA	NA	NA	NA	NA	0.73	–

Notes: Significant F_{ST} values ($P < 0.05$) are in bold. Abbreviations: TMA = Tres Marías Archipelago; BCS = Baja California Sur; MICH = Michoacán; GRO = Guerrero; OAX = Oaxaca; JAL = Jalisco; NAY = Nayarit; SIN = Sinaloa; NWM = Sonora, Sinaloa, Nayarit, and Jalisco; MAINLAND = all continental populations except Sinaloa.

Hartl and Clark 1997); however, for *I. pustulatus*, our F_{ST} values were not significant for the GRO vs. TMA and GRO vs. OAX comparisons (Table 3), which may be an effect of small sample sizes or of an incomplete representation of the allelic variation in our determined populations (Holsinger and Weir 2009).

AMOVA results showed that most of the genetic variation in *C. cardinalis*, *V. hypochryseus*, and *I. pustulatus* was explained by differences among populations within groups (59.93%, 74.04%, and 99.10%, respectively). However, genetic variation resulting from differences between TMA and mainland populations was also considerable for *C. cardinalis*, *V. hypochryseus*, and *I. pustulatus*; for *T. rufopalliatus* only, most of the genetic variation was explained by differences among populations within groups (Table 4).

Colonization Patterns

Our estimates for the sea level and coastline of the west coast of Mexico during the Pleistocene showed that the coastline distance between the islands of the TMA and the mainland was ~25 km, contrasting with the current distance of ~95 km (Figure 1). Even though, during glaciations, sea level lowered and rose cyclically, leading to multiple opportunities for TMA colonization, our results testing several island colonization scenarios, involving different diversification times (Figure 4; Supplemental Material Appendix B), suggested that the most favorable colonization route to the islands for all 4 species in the present study was from NWM to the islands and occurred ~120 kya. Our estimate of the ratio of variance to mean divergence times was $\Omega = 0.008$ (95% quartiles: 0.000–0.075), which suggests a single divergence event for all species; moreover, the number of divergence times across taxon pairs was coincident with a single diversification event that took place 120 kya ($\psi = 1.31$, PP = 0.77; Figure S6).

DISCUSSION

Bird Colonization and Differentiation in Oceanic Islands

Most oceanic islands like the TMA have been colonized by biotas from the mainland, resulting in the appearance of isolated populations that later may experiment with evolutionary diversification and speciation. Allopatry has been recognized as the default model for speciation in oceanic islands (Ronquist and Cannatella 1997, Nylander et al. 2008), because geographically isolated populations are not connected by gene flow, and both genetic drift and natural selection have resulted in divergence (Harrison 2012).

In certain cases, however, populations are allopatric but still geographically close enough for exchange of occasional migrants due to the dispersal capabilities of the taxa involved (Servedio 2010) or may show evidence of cyclical gene flow and isolation due to climate change (Barker et al. 2012). Each of our 4 study species showed clear genetic divergence between TMA and mainland populations, although insularity as an effective barrier limiting gene flow is different among them. For *C. cardinalis* and *T. rufopalliatus*, gene flow is highly reduced and lineages are highly divergent; whereas for *V. hypochryseus* and *I. pustulatus*, gene flow and/or incomplete lineage sorting might best explain the observed patterns.

This evolutionary differentiation is coincident with data observed in other bird species from the TMA, such as the Yellow-headed Parrot (*Amazona oratrix*; Eberhard and

TABLE 4. Analysis of molecular variance (AMOVA) between Tres Marías Archipelago and mainland populations, and among populations for each species.

Species	Source of variation	df	Sum of squares	Variance components	Percentage of variation	Fixation indices [a]
Cardinalis cardinalis	Among groups	1	150.43	6.30	35.44	$F_{CT} = 0.35$*
	Among populations within groups	2	344.72	10.65	59.93	$F_{SC} = 0.93$**
	Within populations	57	46.84	0.82	4.62	$F_{ST} = 0.95$**
Turdus rufopalliatus	Among groups	1	105.47	5.43	79.18	$F_{CT} = 0.79$*
	Among populations within groups	2	9.40	0.31	4.56	$F_{SC} = 0.22$**
	Within populations	48	53.54	1.11	16.27	$F_{ST} = 0.84$**
Vireo hypochryseus	Among groups	1	78.20	0.81	11.14	$F_{CT} = 0.11$*
	Among populations within groups	1	20.99	5.41	74.04	$F_{SC} = 0.83$*
	Within populations	31	33.56	1.08	14.82	$F_{ST} = 0.85$**
Icterus pustulatus	Among groups	1	8.09	–0.82	–34.63	$F_{CT} = -0.35^{ns}$
	Among populations within groups	2	37.31	2.33	99.10	$F_{SC} = 0.74$**
	Within populations	28	23.45	0.84	35.53	$F_{ST} = 0.64$**

[a] ns = not significant ($P > 0.05$); *$P < 0.05$; **$P < 0.001$.

Bermingham 2004) and the Mexican Parrotlet (*Forpus cyanopygius*; Smith et al. 2013), in which TMA and mainland populations were reciprocally monophyletic, as well as in previous analyses of some of our study species (e.g., Smith et al. 2011, Montaño-Rendón et al. 2015). This pattern of insular divergence also occurs in other islands in different geographic settings, including the Canary Islands (Marshall and Baker 1999, Lifjeld et al. 2016), Taiwan (Wang et al. 2016), and Guadalupe Island in NWM (Aleixandre et al. 2013). These examples suggest that insularity conditions around the world promote divergence by reducing gene flow between mainland and island populations.

Evidence suggests that in many cases of island bird speciation, the divergence of insular lineages has been the result of isolation due to Pleistocene climatic fluctuations (e.g., Bird et al. 2005). Once populations have been isolated, divergence of island biotas may be enhanced by low rates of colonization sustained for long periods (Losos and Ricklefs 2009), even when some populations may have been connected intermittently to their neighboring mainland populations during glaciations (Wang et al. 2016).

Concerted Colonization and Genetic Differentiation in the TMA

Although divergence dates varied among the groups of populations of our 4 study species, all splits occurred during the Pleistocene. Our analyses, however, support a simultaneous divergence for the 4 species in the islands (see below), although discrepancies in divergence times were observed and could be due to heterogeneity in substitution rates among species (Harrison and Larson 2016) or to a founder effect (Baker and Moeed 1987). It is known that rates of non-synonymous substitution in mitochondrial coding sequences of island birds are apparently higher than those observed in close relatives from the mainland (Johnson and Seger 2001, Smith and Klicka 2013), which may be the result of an increased fixation of nearly neutral mutations produced by low effective population sizes (Woolfit and Bromham 2005), which is expected in populations that undergo a genetic "bottleneck," affecting divergence estimates that assume uniform mutation rates.

The observed divergence pattern in birds has been found on other islands, including Hainan (Wang et al. 2016), the Philippines (Hosner et al. 2014), the Azores (Dietzen et al. 2006), Corsica and Sicily (Griswold and Baker 2002); and in other taxa inhabiting islands, like frogs (Barker et al. 2012), lizards (Cox et al. 2010), and plants (Wright et al. 2000). This could be because glaciations during the Pleistocene promoted population fragmentation in these taxa, resulting in rapid rates of diversification and speciation (Hewitt 1996, Avise and Walker 1998, Weir and Schluter 2004). Pleistocene climatic oscillations allowed periodic increases and decreases in landscape connectivity by forming bridges and barriers between mainland and archipelagos, resulting in a long-term isolation of populations (Bird et al. 2005, Hosner et al. 2014).

Haplotype networks for the 4 species showed clear geographic and genetic structure between island and mainland populations. The island population of *C. cardinalis* was recovered as closely related to populations from BCS instead of NWM. For *T. rufopalliatus*, the network showed admixture from NWM and MICH+GRO, probably because of incomplete lineage sorting or

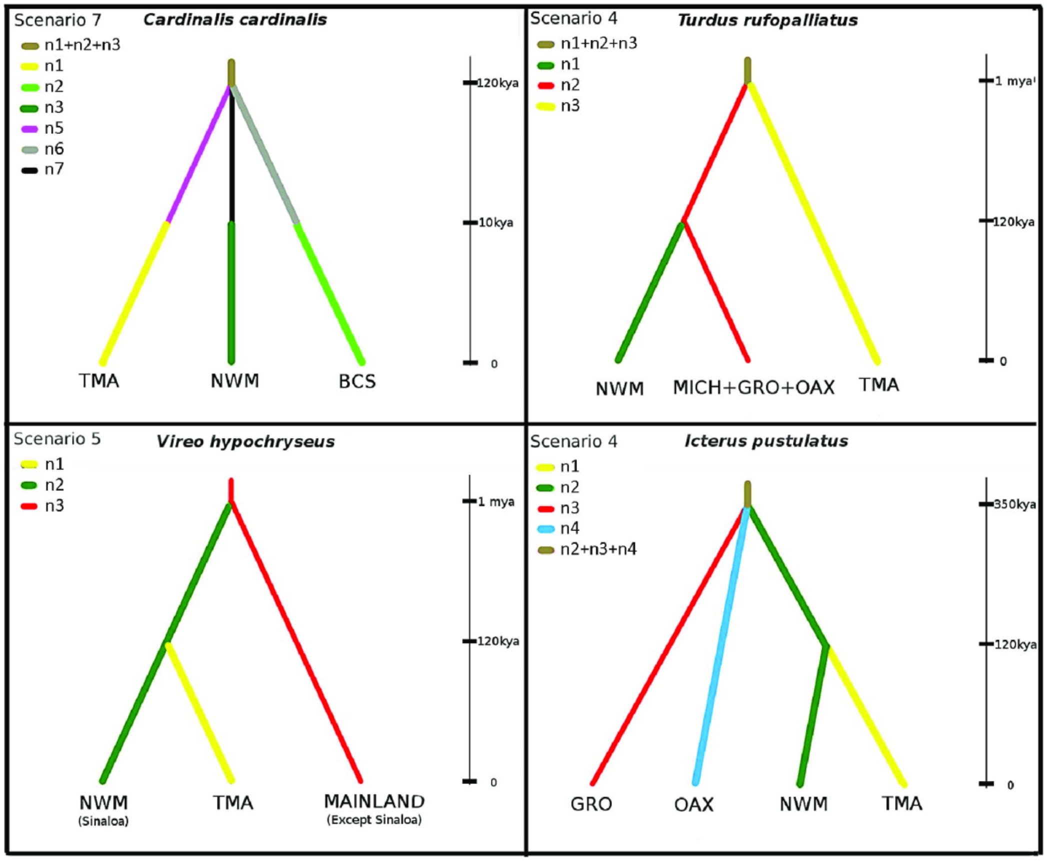

FIGURE 4. Highest-probability scenario tested for colonization of the Tres Marías Archipelago by each study species: (**A**) *Cardinalis cardinalis*, (**B**) *Turdus rufopalliatus*, (**C**) *Vireo hypochryseus*, and (**D**) *Icterus pustulatus*. Population abbreviations are defined in the text and in captions of Figures 1 and 2.

secondary contact, as previously suggested (Montaño-Rendón et al. 2015). For *V. hypochryseus*, we found that the population from TMA is closely related to samples from Sinaloa, suggesting either (1) that this area within NWM has acted as a source of individuals for the TMA when favorable conditions during the Pleistocene and sea-level changes led to individual interchange between mainland and islands (Zweifel 1960, Kodandaramaiah 2009); or (2) alternatively, that there is ongoing gene flow. Lastly, for *I. pustulatus*, we found 2 mutational changes between mainland and island haplotypes, suggesting a recent origin for the TMA population.

Although some of our AMOVA results should be interpreted carefully, given our sample sizes, for *T. rufopalliatus* and *I. pustulatus* most of the genetic variation is not allocated between TMA and mainland groups, but in variation within groups, which suggests that mainland populations were isolated in the past (Arbeláez-Cortés et al. 2014a, Montaño-Rendón et al. 2015).

We obtained low values of nucleotide diversity and, in general, high haplotype diversity values that suggest demographic changes produced by population bottlenecks followed by rapid population growth and accumulation of mutations (Grant and Bowen 1998). It is widely accepted that newly founded island populations support lower genetic diversity than their mainland counterparts as a result of increased rates of drift and inbreeding due to the reduced effective size of island populations (e.g., Frankham 1997, Illera et al. 2016). This is concordant with patterns reported by Nadachowska-Brzyska et al. (2015), who found that most population declines and increases occurred within the past million years or so, as a direct consequence of global climate changes (Hewitt 2000, Nadachowska-Brzyska et al. 2015), as supported by our demographic analyses and neutrality tests. Overall, genetic differentiation and demographic results supported the hypothesis that the 4 species that currently have an apparently continuous distribution were probably isolated during the Pleistocene.

Climatic Changes and Connectivity of Islands to Mainland

Our estimate of the geographic position of Mexico's western coastline during the Pleistocene is concordant with that of Zweifel (1960). Our analyses of colonization routes better support the hypothesis of colonization of the TMA from NWM populations, apparently as a result of a population expansion when environmental conditions were favorable. Our best-supported scenario, dispersal to the TMA, indicates that a single diversification event occurred ~120 kya, which is the estimated date when the TMA emerged (McCloy et al. 1988). This pathway has also been suggested by Casas-Andreu (1992) to explain how other insular flightless vertebrates (reptiles and amphibians) colonized the TMA. These authors concluded that TMA populations have a higher biogeographic affinity to coastal populations from Sinaloa, Nayarit, Jalisco, and Colima (highly similar to our NWM). In particular, amphibians are unlikely to disperse over oceanic barriers, given their inability to tolerate the osmotic stress by saltwater (de la Torre et al. 2010). However, although our analysis better supported an NWM origin for all of our species, genetic patterns found in *I. pustulatus* also suggest other alternatives. For example, populations of some species in the TMA may be derived from the area extending between Colima and Oaxaca, which has previously been suggested in regard to the odd biogeographic pattern found in *A. oratrix* (Stager 1957). Migration could also occur from the islands to the mainland, following a pattern known as upstream dispersal (Filardi and Moyle 2005, Bellemain and Ricklefs 2008). We tested this hypothesis for *V. hypochryseus*; however, the most supported scenario suggested colonization from NWM to the TMA.

Our results demonstrate that island populations close to the mainland are in significant stages of genetic differentiation and that the processes of population dynamics on islands are different from those occurring on the nearby mainland (see Jensen et al. 2013). However, our analyses also suggest that insular areas may have taxa with different biogeographic origins, supporting complex scenarios for the assemblage of species, which may take advantage of geographic conditions imposed by Pleistocene climatic changes, as in the case of the TMA avifauna.

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CAPÍTULO III

ECOLOGY AND GENETICS DRIVE BIRD SONG EVOLUTION IN THE TRES MARÍAS ISLANDS, MEXICO

Ecology and genetics drive bird song evolution in the Tres Marías Islands, Mexico

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Abstract

Bird songs can act as a reproductive barrier due to their function in mate attraction. Here, we aimed to analyze how genetics, morphology, habitat type, and biogeographic history could shape bird songs in four passerine bird species of the Tres Marías Islands Archipelago (TMA). We tested whether bird song differences are related to morphological or ecological differences (temperature, precipitation and habitat type) between TMA and mainland. We also searched for evidence of migration between TMA and mainland by comparing repertoire sizes and genetic fixation index (F_{ST}). Then, through a mixed effects models analysis, we explored if the differences in acoustic space that bird populations use for communication is best explained by morphology, genetics, environmental conditions, habitat type, geographic isolation, or interactions among them. We found that ecological characteristics are affecting bird song differences between TMA and mainland populations. This could be by directly affecting sound transmission performance or indirectly as a result of morphological differences. Genetic F_{ST} values and syllable sharing index suggests low cultural and genetic flow between TMA and mainland. Thus, the isolation of TMA populations is also an important factor that contributed to bird song divergence in these islands. Due to a reduction in biological diversity, the acoustic space available for recent colonizers could be shifted or higher than in mainland. Genetic evidence suggests that TMA populations have been isolated for thousands of years. Thus, the combination of time since colonization event, founder effect, ecological differences, low migration rates, and probably lower sexual selection, have been favoring the fixation of different traits in TMA populations that are evolving independently from mainland.

Key words: Acoustic window, Colonization, Isolation, Founder effect, Pleistocene.

Introduction

Bird song divergence is an important driver of bird evolution (Irwin et al., 2001; Podos and Warren, 2007; Mason et al., 2017). In many species, song divergence often precedes that of other genetic and morphological characters (Potvin and Clegg, 2015). Because bird songs can act as a reproductive barrier due to their function in mate attraction, they are prone to be under sexual selection leading to assortative mating (Catchpole and Slater, 2008; Price, 2008). As multiple factors constrain bird songs, such as genetics, morphology, ecology, and sexual selection, evolutionary biologists are discouraged from using them in phylogenetics (McCracken and Sheldon, 1997). However, in recent years, the use of bird songs in evolutionary research has increased considerably, and now we are able to explore the significance of acoustic divergences either as a pre-mating barrier, or in reinforcing reproductive isolation (Wilkins et al., 2013).

Bird songs have phylogenetic information because vocalizations and cultural learning are constrained by auditory predisposition, characteristics of brain regions, and morphology, all of which are genetically defined (Sober et al., 2008; Ali et al., 2013; Bertram et al., 2014; Wheatcroft and Qvarnström, 2015). Thus, mutations in genes related to vocal learning, song production, or morphology may produce either bird song changes, or inaccurate imitation of tutor´s song (Haesler et al., 2007; White, 2010). Comparisons of bird song syllable repertoires between populations also may allow reconstruction of possible colonization events via syllable sharing or reduction providing information of cultural flow or founder effect (Baker and Jenkins, 1987; Potvin and Clegg, 2015). This comparison allows to analyze if population divergence has resulted from mechanisms of isolation and differentiation by cumulative genetic history, or by environmental and ecological variables acting over populations (Payne, 1986; McCracken and Sheldon, 1997).

However, colonization events potentially lead to bird song differentiation when populations are founded by a small group of individuals, which carry only a limited amount of song variation to the new population (founder effect; Baker and Jenkins, 1987). These phenomena frequently produce a syllable reduction in the repertoire of the newly founded population (Lynch and Baker, 1986; Baker and Jenkins, 1987; Baker et al., 2001). For isolated and small sized populations of oscine birds (birds that learn their songs), such differences may be generated by errors during song learning from one generation to other (Lynch, 1996; Podos and Warren, 2007), or by syllable innovation and cultural transmission that may lead to important differences between populations in a relatively short time (Baker et al., 2003). Hence, such differences have higher chance to get fixed in the population due to its small size (Futuyma, 2005). Alternatively, in islands close to mainland (or source population), the amount of gene flow and cultural flow may reduce divergence, leading to homogenization or reducing divergence rates (Baker and Jenkins, 1987; Lynch and Baker, 1994).

Morphology and habitat are among the main factors related with variation in bird song features. Birds with larger bills produce songs with narrower frequency bandwidths and lower rates of syllable repetition (Lynch and Baker, 1986; Podos, 2001; Huber and Podos, 2006). Comparisons of bird songs between island and mainland populations should consider that frequency differences due to bill size could be high because many island bird populations present longer bills than mainland populations, even without differences in body size (Clegg and Owens, 2002). Longer bills have probably resulted from thermoregulation and water balance adaptations: a longer bill lead birds to dissipate the excess heat through the bill surface without water loss, which is advantageous in environments with limited fresh water (Greenberg and Danner, 2012; Luther and Danner, 2016). On the other hand, bill shape variations in island populations may result from ecological competition release, and different arrays of food resources (Boag and Grant, 1981; Grant and Grant, 2006). In addition, island bird populations frequently have larger body sizes than their mainland counterparts (Olson et al., 2009). Previous studies observed a relationship between body size and bird song features, such as frequency and temporal structure (García et al., 2014; Mason and Burns, 2015), in which birds with larger body sizes emit songs with lower frequencies and narrower frequency bands than small body-sized birds (Wallschläger, 1980; Ryan and Brenowitz, 1985; Mason and Burns, 2015).

Differences in environmental conditions and habitat type have been also suggested to shape bird song frequencies and syllable types by favoring or reducing sound transmission (Morton, 1975; Slabbekoorn and Smith, 2002; Seddon, 2005). Habitats with denser vegetation should favor lower frequency songs with narrower frequency ranges, longer notes and longer inter-element intervals that are less prone to attenuation; while the opposite is expected in open habitats (Chapuis, 1971; Richards and Wiley 1980; Boncoraglio and Saino, 2007). Particularly for Neotropical dry forest, precipitation is highly important for determining the habitat structure (Stotz et al., 1996; Rzedowsky 2006), which, in addition with other ecological factors, is correlated with vegetation type (*i. e.*, temperature, soil, light and site conditions; Gentry, 1995; Spano et al., 1999; Li et al., 2004; Rzedowsky, 2006; Gao et al., 2017; Yan et al., 2017). Tropical dry forest has a gradient in precipitation and temperature along the Neotropics (Stotz et al., 1996). Moreover, high frequencies tend to be more attenuated than lower frequencies in hot or humid conditions (Catchpole and Slater, 2008). Thus, bird song frequencies can be related with precipitation and temperature of the habitat.

Sensory drive is a process that causes evolutionary change in communication systems (in mechanisms to detect and discriminate signals), as well as the structure of the signals themselves, reducing attenuation or degradation (Endler, 1992; Boughman, 2016). Thus, the environment in which communication takes place affects the transmission of the signal (Boughman, 2016). The "acoustic window", represents the space available of acoustic parameters for signal evolution in a given taxon in a given habitat, considering the structure of the habitat, ambient noise, presence or absence of predators or other species with acoustic communication (Wilkins et al., 2013). In addition with differences in morphology (bill and body size) and phylogenetic history, this could shape bird song evolution (Wilkins et al., 2013). If a species spends a long time in a particular habitat with particular sound transmission characteristics, then the sensory systems can evolve to best match the new environmental conditions (Endler, 1992). Hence, colonization of new areas, like islands, frequently constrains founders to new habitat structure and food resources, along with differences in genetics, morphology, and environmental conditions between island and mainland, could generate differences in the acoustic window and therefore promoting bird song divergence or even speciation. However, even when bird songs or syllables can perform well under certain habitat conditions, they are probably not favored by sexual selection and therefore disappear from population through female choice (Endler, 1992; Boughman, 2016), other variation type is produced when females favor different syntax of the same elements, resulting in different songs (Grant and Grant, 1996; Cody et al., 2016; Ivanitskii et al., 2017).

The Tres Marías Islands (TMA) is an archipelago located in the central western coast of Mexico, and presents an ideal opportunity to study the relation of genetic and morphological divergence in the evolution of bird songs in insular passerine birds. The TMA is a volcanic archipelago that, according to stratigraphic evidence, emerged above sea level in the late Pleistocene (McCloy et al., 1988), meaning that land biotas of the islands must have colonized from mainland sources, through founder effect processes. Recent studies suggest that these colonizations occurred approximately 120 thousand years ago (kya), when mainland and TMA where closer due to a sea level reduction (ca. 100 m below current level) during the Pleistocene, and after sea level rose again, TMA populations got isolated (Zweifel, 1960a; Wilson, 1991; Ortiz-Ramírez et al., 2018). This event reduced gene flow and likely enhanced genetic and morphological divergence between TMA and mainland (Wilson, 1991; Leisler and Winkler, 2015; Ortiz-Ramírez et al., 2018).

Many passerine birds from TMA have longer bills and bigger body sizes than their mainland counterparts, apparently due to a combination of evolutionary and ecological factors (Grant 1965a, 1968, 1971). Although vegetation type in both areas is tropical deciduous forest (Ferris, 1927; Rzedowski, 2006), the mainland plant diversity is almost three times higher than TMA (Hahn et al., 2012), and environmental conditions are dryer in the TMA than in mainland. However, the most similar vegetation area as compared to TMA is located along Sinaloa, in the northwestern coast of Mexico (Wilson 1991). In addition, terrestrial bird species richness in TMA is half that in mainland (Hahn et al., 2012).

Here, we aimed to analyze how genetics, morphology, habitat type, and biogeographic history could shape bird songs in four passerine bird species with different ecologies from the western coast of Mexico and TMA. We tested whether bird song differences are related to morphological differences (body size and bill volume) or environmental differences (temperature, precipitation and habitat type) between TMA and mainland. We also searched for evidence of migration between TMA and mainland by comparing repertoire sizes and genetic fixation index. Then, through a mixed model analysis, we explored if the differences in acoustic space that bird populations use for communication is best explained by morphology, genetics, environmental conditions, habitat type, geographic isolation, or interactions among them. Our main goal is to improve our understanding of the evolution of bird songs in isolated populations, as well as to explore its relevance for island biodiversity by promoting assortative mating, limiting gene flow between populations, and favoring speciation.

Methods

Study area. -- The Tres Marías Islands Archipelago (TMA) consists of four volcanic islands (María Cleofas, María Magdalena, María Madre, and San Juanito) that are located offshore the central western coast of Mexico, approximately 132 km west of San Blas, Nayarit, Mexico (21.778N–21.258N, 106.698W–106.198W; Figure 1). The elevation ranges from sea level to 650 m at the highest point in María Madre. The islands are covered mainly by tropical deciduous and semi-deciduous forest mixed with thorn scrub, mangroves, and cacti. The rainy season occurs from June to December (Grant 1965a; Hahn et al., 2012). According to stratigraphic evidence María Madre, the highest island, emerged above sea level in the late Pleistocene (McCloy et al., 1988). Apparently sea level fluctuations during glaciations of the Pleistocene caused that TMA and mainland where closer (~25 km contrasting with the actual distance of ~95 km; Figure 1) or even connected (Zweifel, 1960a; Wilson, 1991).

Taxon sampling. -- We analyzed four passerine bird species for which previous studies have reported genetic divergence between TMA and mainland populations: *Cardinalis cardinalis* (Smith et al., 2011; Smith and Klicka 2013; Ortiz-Ramírez et al., 2018), *Turdus rufopalliatus* (Montaño-Rendón et al., 2015; Ortiz-Ramírez et al., 2018), *Vireo hypochryseus* (Arbeláez-Cortés et al., 2014; Ortiz-Ramírez et al., 2018), and *Icterus pustulatus* (Cortés-Rodríguez et al., 2008; Ortiz-Ramírez et al., 2018). All of them apparently colonized TMA simultaneously ~120 kya (Ortiz-Ramírez et al., 2018), thus we have a minimum date to set as maximum isolation period or limited gene flow between TMA and mainland, particularly northwestern Mexico (hereafter NWM) which is the closest relative population of TMA populations for three of the four species analyzed; only for *I. pustulatus*, Oaxaca and Guerrero populations are closer related to TMA than to NWM (Ortiz-Ramírez et al., 2018).

Morphological measurements. -- We measured specimens of the four selected species in scientific collections in Mexico (see acknowledgments). We obtained three measurements from the bill (length, depth, and width), the length of the wing, and the length of the tarsus. All bill measures were performed with a Mitutoyo Absolute Digimatic digital caliper (precision of 0.1 mm), bill depth and bill width were taken at the anterior border of the nostrils; wing chord was measured from the carpal joint to the tip of the longest primary feather without flattening the wing; and tarsus length was measured from the tibiotarsus joint, to the midpoint of the distal edge of the scute at the opposite end. Although there is evidence of female song in *I. pustulatus* (Price et al., 2008) and *C. cardinalis* (Ritchison, 1986; Yamaguchi, 1998), we considered only songs of males. Thus, in order to eliminate variation in bill size due to age and sex, we considered only adult (according to specimen skull ossification) male individuals. Body mass was recorded directly from specimen tags. We removed the influence of body size from bill size following Huber and Podos (2006). First, we obtained the residuals for each species, then we estimated a linear regression between each bill measurement (depth, with and length) against the first principal component of the tarsus length, wing chord and body mass measures for each species. Once we obtained the residuals of bill measures we estimated bill volume as follows:

$$Vol = \frac{\pi \times \frac{1}{2} billdepth \times \frac{1}{2} billwith \times billlength}{3}$$

We compared bill volume residuals using Kruskal-Wallis tests. To analyze how bird songs response to morphology variation, we performed mixed effect models (see mixed effect models analyses below).

Climatic variables. -- We obtained the environmental variables for the sampling point of each recording using the lat/long coordinates and the WorldClim climatic environmental layers (Fick and Hijmans, 2017), with a resolution of 0.5 minutes using the function "*gedData*" of the "raster" R package (Hijmans, 2018). We divided the 19 variables in two modules: 1) temperature (bio1-bio11); and 2) precipitation (bio12-bio19). We then performed a Principal Component Analysis (PCA) to reduce dimensionality in each module. Once we obtained principal components, we estimated the environmental hypervolume for each individual using the Gaussian method as implemented in the "*hypervolume*" R package (Blonder et al., 2014, 2018). We compared environmental hypervolumes using Kruskal-Wallis tests and identified the pairwise differences with the Dunn method (Dunn, 1964).

Acoustic measurements and acoustic hypervolume. -- We obtained all available song recordings covering the distribution of the four studied species in western Mexico, including the TMA, from digital sound collections (see Appendix I). We improved our sampling by our own field recordings in Nayarit, Jalisco, Oaxaca, Sinaloa, and TMA (Appendix I). To standardize our samples, recordings with sampling size of 24 bits were transformed to 16 bits; sampling rate of 48 kHz to 44.1 kHz; and for recordings with two channels, only the channel with the best signal-noise ratio was used. Bird songs were selected in Raven Pro 1.4 (www.birds.cornell.edu/raven) and then selection tables were imported in R using "warbleR" (Araya-Salas and Smith-Vidaurre, 2017).

We performed an autodetection of the notes in each bird song selection with the "*autodetec*" function with the following parameters: bandpass filter between 1.5-6 kHz, window overlap of 90% and window length of 1024. For those recordings that were not autodetected, we selected notes manually with the function "*manualoc*", and added them to the autodetection database. We obtained notes and songs catalogs for visual inspection with the "*catalog*" function of the recordings for each species according to the genetic groups previously identified in the literature (Ortiz-Ramírez et al., 2018). We then measured all selections for spectrogram parameters of notes with the function "*specan*", with the same parameters used for autodetection (see appendix II for the measured variables list). Variables were grouped in three modules: 1) duration; 2) frequency, and 3) Shape of notes (roundness, flatness or peak shape). All acoustic measurements were made with warbleR. We estimated the acoustic hypervolume of each individual for the three acoustic modules using the acoustic variables without collinearity (see below statistical analyses). First, we scaled and centered the variables with the "*scale*" function of the R base (R Core Team, 2019), and then performed the Gaussian method as implemented in the "*hypervolume*" R package (Blonder et al., 2014, 2018).

Vocal repertoire sizes. -- We defined syllables as a composition of one or two notes which are a continuous trace in a spectrogram or the smallest unit in a song (Catchpole, 2000). We performed an automated classification of notes using the function "*df_DTW*" of "warbleR" package to obtain the acoustic dissimilarity among the dominant frequency contours of notes using the dynamic time warping of the "*dtwDist*" function from the "dtw" R package (Giorgino, 2009). We then used the "*tsne*" function of the "Rtsne" R package (van der Maaten and Hinton, 2008; van der Maaten, 2014; Krijthe, 2015) to visualize classifications and reclassified them manually if necessary, according to visual inspection of the catalogs previously created. Once the note classification was satisfactory, we counted the note types particular to each genetic group and each geographic area, as well as the shared ones between genetic group and between geographic areas. Simple enumeration of syllables is a reliable method for estimating repertoire sizes of species with small repertoires but not for species with large repertoire sizes (Botero 2008). Thus, we needed to estimate how complete is our syllable sample, so we performed accumulation and rarefaction curves (Chao et al., 2014) to estimate the effort in the estimations of repertoire sizes for each species's genetic group. Then, we employed syllable types presence/absence as incidence data in the "iNEXT" package for R (Hsieh et al., 2019).

Genetic flow and cultural flow. -- Gene flow between TMA and mainland was assessed from F_{ST} values from previous genetic studies (Ortiz-Ramírez et al., 2018). Low gene flow between populations was assumed when F_{ST} values were high (>0.25 according to Hartl and Clark, 1997). Vocal differences which arose in island populations following a colonization event could have a role in bird evolution (Baker, 2012). Syllable sharing between populations could be interpreted as cultural flow (Jenkins, 1978; Rivera-Gutiérrez et al., 2010; Price and Yuan, 2011; Lachlan et al., 2013). We estimated pairwise syllable sharing between genetic groups for each species, following Rivera-Gutiérrez et al. (2010). We used Dice's similarity index (Dice, 1945) as follows: S= 2a/(b+c), where "S" is the similarity between genetic groups, "a" is the number of syllables shared by two genetic groups, "b" and "c" are the syllable repertoire sizes of each genetic group. Values of 0 means no syllable sharing, whereas values of 1 implies total syllable repertoire sharing.

Relationships between body size and bird song frequencies. -- Morphological sizes such as body size and bill size are related with bird song frequencies (Bowman, 1979; Palacios and Tubaro, 2000; Podos, 2001). To explore if bird song frequencies (mean dominant frequency, minimum frequency, mean peak frequency, and dominant frequency range) are related with bill size and body weight (as a proxy of body size). For each species we performed correlations (Spearman correlations) between the mean weight of each genetic group and each frequency variable. Then, we tested their significance by obtaining the P-values for Spearman's rho estimates (Akoglu, 2018) implemented in the "stat*"* package for R with the function "*cor*" (R Core Team, 2019).

Relationships between habitat type and bird song frequencies. -- Differences in habitat type are related with bird song frequencies due to sound transmission (Morton, 1975). Habitats with denser vegetation should favor songs with lower frequency and narrower frequency ranges that are less prone to attenuation; while the opposite is expected in open habitats (Chapuis, 1971; Richards and Wiley, 1980; Boncoraglio and Saino, 2007). We used the WWF ecoregions as a proxy of the habitat structure (Olson et al., 2001). We extracted the latitude-longitude information for each recording locality with QGIS 2.18 (http://www.qgis.org); then, we tested if song frequencies (mean dominant frequency, minimum frequency, mean peak frequency, and dominant frequency range) differed among habitats for all species by performing a Two-way ANOVA.

Mixed effect models. -- To identify redundancy among all the variables measured, we performed collinearity matrices for a visual inspection, and selected variables without collinearity (see Appendix II) according to Variance Inflation Factor (VIF) with the function "*vif*" of the "*usdm*" R package (Naimi et al., 2014). We considered VIF values ≤5, which corresponded to a multiple correlation of 0.9 between each independent variable and all others, this VIF value is more restrictive than the common VIF value of 10, and is recommended for small sample sizes (Menard, 2001; O'Brien, 2007; Hair et al., 2010).

Because our data have nested structure (multiple bird songs measured from multiple individuals from different genetic groups of multiple species), different sample sizes, and because linear regression models do not take phylogenetic relatedness into account, which is likely present between different populations of same genetic group, we proceeded to analyze our data with a mixed-effect models approach (Zuur et al., 2009). We set the acoustic hypervolume as a response variable. Bill volume, environmental hypervolume, latitude (as a proxy of geographic distance), and genetic group were set as explanatory variables; songs where nested in individuals which were nested in species. For the model selection and validation process, we used the top-down strategy following recommendations of Zuur et al. (2009).

Results

Morphological data. -- We measured 205 adult male specimens in total; 33 *C. cardinalis*; 85 *I. pustulatus*; 42 *T. rufopalliatus*; and 45 *V. hypochryseus*. In general, we observed bigger bill volumes from TMA genetic groups than mainland groups in most of the species analyzed. Significant differences in bill volume were found between TMA and mainland genetic groups for *C. cardinalis* (particularly NWM and GRO+OAX); *I. pustulatus* (only GRO); and *T. rufopalliatus*. On the other hand, *V. hypochryseus* did not show any significant difference between TMA and mainland genetic groups (Table 1). Moreover, we explored the existence of bill volume variation among mainland populations in the four species, and found not differences between mainland populations of *C. cardinalis*. However, we found significant differences among all mainland populations for *T. rufopalliatus*, and between NWM and GRO for *I. pustulatus* (Table 2).

Repertoire sizes. -- According to our estimates, most of our syllable sample effort at species level was complete (100%), only for *T. rufopalliatus* the sample coverage was lower (SC=90.5%). However, for genetic groups our estimates of sample completeness were in general insufficient. For *C. cardinalis* or sample coverage was: TMA=96%, NWM=54.3%, OAX=79.8%; for *I. pustulatus*: TMA=40%, NWM=100%, OAX=62.5%; for *T. rufopalliatus*: TMA=61.1%, NWM=88.7%, OAX=45%; and for *V. hypochryseus*: TMA=89.9%, Mainland=98.3%, we were unable to estimate the sample coverage for SIN because we only have one recording for this group (Figures 3-6). Despite the sampling effort, syllable repertoires were analyzed to explore the existence of syllable reduction in TMA populations, probably as a result of founder effect, our results showed that repertoire sizes were lower in TMA than any mainland genetic group for *I. pustulatus* and *T. rufopalliatus;* for the species *V. hypochryseus* we observed that repertoire size between TMA and mainland have almost the same size; and only for *C. cardinalis* repertoire size is higher in TMA than mainland genetic groups (Table 3). However, when we analyzed samples according to the geographic areas they belong, we observed that populations near TMA (particularly Jalisco) have similar repertoire sizes between them for *I. pustulatus* and *V. hypochryseus*. In the one hand, we observed for *T. rufopalliatus* that repertoire sizes are higher in most mainland populations than TMA, but on the other hand, for TMA population of *C. cardinalis* has higher repertoire size than any mainland population (Table 4).

Genetic and cultural flow. -- All F_{ST} values were >0.25 among all genetic groups (see Ortiz-Ramírez et al., 2018). Whereas, syllable sharing between TMA and mainland was high for *C. cardinalis* and *V. hypochryseus*, intermediate for *I. pustulatus*, and low for *T. rufopalliatus* (Table 5). Between TMA and mainland genetic groups it was high for all comparisons of *C. cardinalis*; between NWM-OAX for *I. pustulatus*; moderate for *I. pustulatus* between TMA-NWM; and *T. rufopalliatus* for TMA-OAX and NWM-OAX. All other comparisons were low (Table 5).

Climatic differentiation. -- Once we obtained environmental hypervolumes for each genetic group of the four species and compared them, we observed that in general, environmental conditions differed between TMA and mainland for three of the four species analyzed. Particularly, environmental hypervolume was different between genetic groups of TMA and mainland for *T. rufopalliatus*; *C. cardinalis* from NWM and GRO+OAX; and *I. pustulatus* from NWM and OAX. However, for *V. hypochryseus* our analyses did not show any evidence of environmental hypervolume differences between TMA and mainland groups (Table 6).

Relationship between morphology and song frequencies. -- Our correlations between weight (as a proxy of body size) and bird song frequencies were low but significant for *C. cardinalis* in all frequency measures but mean dominant frequency and dominant frequency range. However, when controlling bill size by weight, both mean dominant frequency and dominant frequency range became significant but acoustic hypervolume became not significant; for *I. pustulatus* only dominant frequency range and acoustic hypervolume were significant with and without controlling by weight; for *T. rufopalliatus* only the dominant frequency minimum and dominant frequency range were not significant, when controlling by weight only the later was not significant; and for *V. hypochryseus* all correlations were significant (Table 7).

Relationships between habitat type and song frequencies. -- Our recording localities corresponded to nine ecoregions that represents the habitat type for each sample: Balsas dry forests, Gulf of California xeric scrub, Jalisco dry forests, Northern Mesoamerican Pacific mangroves, Sierra de la Laguna dry forests, Sinaloan dry forests, Sonoran-Sinaloan transition subtropical dry forest, Southern Pacific dry forests, and Trans-Mexican Volcanic Belt pine-oak forests (see Appendix I). The two-way ANOVA showed that all bird song frequencies (mean dominant frequency, minimum frequency, mean peak frequency, and dominant frequency range) are related with habitat type (Table 8). Most of the dry forests, but the Sierra de la Laguna dry forest, including the ecotone between Pine-Oak forest and Jalisco dry forest, have higher acoustic hypervolumes than dryer habitats that are composed mainly by thorn scrub forest such as Gulf of California xeric scrub or Sonoran-Sinaloan transition subtropical dry forest.

Although the relationship between frequencies and the interaction of species and ecoregions were significant, the species with the highest variation were *C. cardinalis* and *I. pustulatus* (Table 8, Figure 2, Table S1).

The model with lowest AIC value is the one that considers the effect of bill size and environmental conditions, as well as the interaction between them, genetic groups, and habitat type, and species by localities as random effect (Table 7: M4). The best model suggests a strong effect of bill size and environmental conditions. However, genetic difference and habitat type are also significant to explain the acoustic differences among populations.

Discussion

Geographic isolation has a strong influence in the evolution of populations (Mayr, 1942; Price, 2008). Frequently, island populations have a lower genetic diversity than mainland populations due to founder effects, genetic bottlenecks, or genetic drift (Frankham, 1997; Dudaniec et al., 2011). In addition with ecological factors like climate, vegetation type, food resources, and competition, these factors may drive adaptive divergence between populations in different sets of characters like morphology, genetics, and vocalizations (Dudaniec et al., 2011).

Divergence in characters that are involved in mate choice, like bird songs, may also result in reproductive isolation upon secondary contact (if geographic barrier disappears) and promote speciation (Edwards, 2005). However, multiple factors affect bird songs in frequency features and syllable composition. Thus, the analyses of how the divergence observed in morphology and genetic characters between TMA and mainland populations (Grant, 1965a, 1968; Cortés-Rodríguez et al., 2008; Smith et al., 2011; Smith and Klicka 2013; Arbeláez-Cortés et al., 2014; Montaño-Rendón et al., 2015; Ortiz-Ramírez et al., 2018), and the interaction of environmental conditions, vegetation type, and geographic isolation, are modeling bird songs evolution in TMA will increase our knowledge of avian evolution.

Morphological differences

Differences in bird body size between mainland and island counterparts have been widely studied (Olson et al., 2009; Dudaniec et al., 2011; Danner et al., 2014). Although birds do not show recognizable trends in body size for island populations in all species (Clegg and Owens, 2002), recent studies at global scale have suggested that, in general, island bird assemblages have larger body sizes than their mainland counreparts (Olson et al., 2009). Particularly, species inhabiting TMA are frequently larger in some measurements like wing, tail, and tarsus, but the most general island trend is commonly observed in bill size and shape (Grant, 1965a, 1968). In our study, we observed a variety of results. Once we eliminate the effect of body size from bill measures, we confirmed the bigger bill size pattern for *T. rufopalliatus* and *C. cardinalis* However, for *I. pustulatus* and *V. hypochryseus* we found no differences between TMA and mainland populations.

There are different hypotheses proposed to explain such differences in bill size and shape in islands. One is explained by intra-specific competition Such as ecological segregation due to differences in foraging behavior or diet to avoid competition (Smith, 1990). Many species with larger bills are able to exploit a wider range of food items (Grant, 1968). Thus, species that colonize new areas with different environmental conditions are under different ecological selection pressure that could increase divergence between populations in relatively short time (Reznick and Ghalambor, 2001; Clegg et al., 2008; Rundell and Price, 2009). If there is divergent selection pressure over such traits, then it can generate reproductive isolation (Grant, 1985; Rundell and Price, 2009; Ortiz-Barrientos, 2016). Evidence found in other island systems like the Galapagos Islands Darwin's finches, support that individuals with longer bills have better success when competing for territory, and females with longer bills have higher fitness (Grant, 1985). This hypothesis could apply for *T. rufopalliatus* and *C. cardinalis.* Thus, the bill size differences could be the result of better success of individuals with larger bills in TMA. In that way, this explanation is proposed as a mechanism for speciation in islands (Rundle and Nosil, 2005; Schluter, 2009).

Other explanation is the so called “island rule” (Foster, 1964; Van Valen, 1973), which points out that smaller species become larger whereas smaller species become larger on islands compared with their mainland counterparts (Foster, 1964; Gaston et al., 2008). Studies show that in some bird species, body and bill sizes in islands vary according to this rule, particularly short-billed birds tend to increase bill length, whereas long-billed forms tend to decrease their bill sizes (Clegg and Owens, 2002). Which is not highly different from the former.

A recent explanation suggests that bird bills play an important role in thermoregulation, particularly on areas with limited fresh water sources, like many oceanic islands (Clegg et al., 2002; Greenberg et al., 2012). Heat loss by bill surface may be common among birds (Tattersall et al., 2009), and particularly for coastal populations, heat loss without evaporation is advantageous, thus larger bills would allow birds to dissipate the excess of heat avoiding dehydration (Greenberg and Danner, 2012; Greenberg et al., 2012).

For TMA populations, ecological segregation and thermoregulation could be explaining the morphological variation that we found, given that vegetation and fauna that inhabits there are different from the one from mainland (Ferris, 1927; Casas-Andreu, 1992; Hahn et al., 2012). Apparently, food resources used by these species in TMA are different from those used in mainland. For example, coloration is highly related with the food habits. Specially for red, yellow, and orange colors, those depend on carotenoids which are obtained from diet (Fox, 1979; Goodwin, 1984). Grant (1965b) observed in TMA that *C. cardinalis, T. rufopalliatus,* and *V. hypochryseus* are more drab in color than mainland ones probably as a result of limited resources or due to the absence of closely related species. However, according to our results, the heat loose through bill surface hypothesis is very feasible and is concordant with the differences in environmental conditions in bill size observed herein. Thus, our results could be explained by ecological (food availability and environment) differences between areas.

Syllables and repertoire sizes

Cultural traits such as bird songs are affected by founder effect, mutation, drift and selection (Cavalli-Sforza et al., 1982; Lynch and Baker, 1986). The study of such cultural traits in isolated populations is interesting because the pattern is not obscured by immigration between populations, and is easier to explore the forces acting on song evolution (Lynch and Baker, 1994). Colonization history of TMA from a sea level reduction and posterior isolation of populations offers an exceptional opportunity to explore these phenomena given that we have an estimate of 120kya since colonization (Zweifel, 1960b; Potvin and Clegg, 2015; Ortiz-Ramírez et al., 2018). If populations are isolated for a long time, they will tend to diverge as a result of different mutations arising in each population. However, if migration between populations is high, then the divergence rate can be slowed according to the degree of migration between island and mainland (Lynch and Baker, 1986, 1994).

The degree of bird song repertoire sharing decreases with distance, migration rate and/or time, and could indicate the degree of population isolation (Baker et al., 2001; Rivera-Gutierrez et al., 2010; Pipek et al., 2018). However, comparisons of bird songs between mainland and island of recent colonization, usually show a reduction in syllable diversity via founder effect, cultural drift, or loose of syllable types due to inefficient sound transmission in the new environment (Baker and Jenkins, 1987; Lynch and Baker, 1994; Baker et al., 2006; Lachlan et al., 2013). Thus, the differences between island and mainland populations may reflect the colonization history (Spurgin et al., 2014). Our syllable sharing results suggest a high cultural flow between TMA and mainland for *C. cardinalis* and *V. hypochreus*, and low for *T. rufopalliatus* and *I. pustulatus*. However, our syllable samples sizes were low, thus we cannot make conclusions from this analyses. The pattern found in different islands around the World is that syllable reductions are present in the repertoires. For example, Baker (1996) found that island populations have a syllable diversity reduction in three bird species. He also observed (Baker 2012) in the white-eye *Zosterops lateralis* that in island and mainland populations found 15 km away, songs are moderately differentiated and island population has lower syllable diversity. In other Atlantic islands, Lynch and Baker (1986b) analyzed syllable pools and found a strong negative correlation between syllable pool and geographic distance among populations. They concluded that differentiation among them has been influenced by colonization and suggested a possible route to the islands by the pattern of syllable sharing. In that way, this historical model explains how bird song differences corresponded to the time since population founding or expansion (Payne, 1981). Potvin and Clegg (2015) estimated the number of syllables shared between populations after founder events and found a syllable reduction that corresponded to the number of founder events. Our results for *T. rufopalliatus* and *I. pustulatus* are concordant with the hypothesis of syllable reduction due to founder effect. Especially for *T. rufopalliatus* in which the closest mainland areas to TMA (Nayarit and Jalisco) have three to fourfold the syllable diversity observed in TMA.

However, empirical evidence in other species shows that syllable diversity in island populations are not always lower than mainland populations (Baker, 2014; Potvin and Clegg, 2015). For example, Hamao (2013) reported that in the Old-World warbler *Cettia*, syllable repertoire is the same size or very similar between island and mainland populations. We also observed this pattern in *V. hypocrhyseus*, from which previous genetic studies showed evidence of probable recent migration between Sinaloa and TMA (Ortiz-Ramírez et al., 2018). This genetic flow could be associated with cultural flow that homogenized repertoire sizes between island and mainland population. Other explanation is that due to its relative simple repertoire, TMA colonizers, since TMA foundation, could carry on a large amount of the mainland repertoire.

Indeed, syllable repertoire sizes can be larger in island than mainland due to lower intra and inter-specific competition in islands, produced by lower species richness and abundance, and subsequently sexual selection could favor the addition of new syllables to the island population repertoire (Baker et al., 2003; Potvin and Clegg, 2015). A few studies revealed that some island birds have larger repertoires than their mainland counterparts (e.g. Kroodsma et al., 1999; Baker et al., 2003). In our study, most of the analyzed species have lower or similar repertoire sizes than the closest mainland populations. Only *C. cardinalis* have a bigger repertoire size in TMA than mainland, but this could be due to higher sexual selection pressure.

Some studies have demonstrated that bird song repertoires evolved under sexual selection pressure (Collins, 2004; Węgrzyn and Leniowski, 2010). If repertoire size correlates with male's age, quality, and/or territory size or quality, then females could prefer mate with males with larger repertoires that would have more experience, bigger body size or good genes for longevity (Catchpole, 1980; Krebs and Kroodsma, 1980; Conner et al., 1986; Kagawa and Soma, 2013; Vaytina and Shitikov, 2019). However, there is not always a relationship between age and repertoire size (Catchpole, 1986; Forstmeier and Leisler, 2004). In addition, song repertoire size could be set by male interactions, thus, syllable types evolve within and between populations according to other selection pressures (Collins, 2004; Lattin and Ritchison, 2009; Singh and Price 2015). Particularly for *C. cardinalis*, males repeat syllables and once song got crystallized they are highly stereotyped (Yamaguchi, 1998).

Males of *C. cardinalis* at London, Ontario have a repertoire size of 12-14 syllable types (Lemon, 1965). We also found 14 syllable types in total from which 12 are present in TMA. If we consider syllables present in BCS and NWM that belongs to NWM clade (Ortiz-Ramírez et al., 2018) they sum a total of 11 syllable types which is similar to TMA repertoire size. Ritchinson (1988) observed that the number of notes per song increase according to interactions with other males. These interactions can explain the syllable repertoires differences between TMA and mainland. Previous studies comparing bird densities between TMA and the adjacent mainland reported a density of birds 35% greater in TMA than mainland (Grant, 1966). Probably the interactions among males in TMA are higher than mainland resulting in a major competition for territory and females. Other studies suggested that females that mate with males of higher repertories have offspring with better viability (Catchpole and Slater, 2008). However, due to our small sample size for *C. cardinalis* we have no confidence of mainland repertoire size, thus we do not discharge the existence of the former pattern in this species too.

Relationship between body size and habitat type with bird song frequencies

Morphological sizes such as body size and bill size are related with variation in bird song frequencies (Bowman, 1979; Palacios and Tubaro, 2000; Podos, 2001), in which birds with larger bills produce songs with narrower frequency bandwidths and lower rates of syllable repetition (Lynch and Baker, 1986;

Podos, 2001; Huber and Podos, 2006). Most of our correlations between bird song frequencies (mean dominant frequency, minimum frequency, mean peak frequency, and dominant frequency range) and morphological measurements were significant, particularly for bill size adjusted by weight. However, for *I. pustulatus* only dominant frequency range and acoustic hypervolume were significant. In general, most of the correlations were low although significant. This suggests that the relationship between body size and bird song frequencies are low. This is contrary with what was found in the Asian barbets where beak length was not correlated with any song feature after controlling by body size (Gonzalez-Voyer et al., 2013). Thus, bird songs are likely affected by other factors such as habitat and environmental conditions.

Differences in habitat type are related with bird song frequencies due to sound transmission (Morton, 1975). Habitats with denser vegetation should favor songs with lower frequency and narrower frequency ranges that are less prone to attenuation; while the opposite is expected in open habitats (Chapuis, 1971; Richards and Wiley, 1980; Boncoraglio and Saino, 2007). We used the ecoregions as a proxy of the habitat structure (Olson et al., 2001), and observed that all frequency attributes measured (mean dominant frequency, minimum frequency, mean peak frequency, and dominant frequency range) are related with habitat type in all species analyzed. In particular, we observed that most dry forests, but the Sierra de la Laguna dry forest, including the Pine-Oak forest and Jalisco dry forest ecotone, have higher acoustic hypervolumes than other habitats which are composed mainly by thorn scrub forest, are characterized by lower height and more open vegetation structure (Gentry, 1995). These findings support the hypothesis that environmental conditions affect the sound transmission (Endler, 1992). High frequencies are prone to be absorbed by environmental conditions like hot or humid conditions (Catchpole and Slater 2008). Our results are concordant with previous studies in which greater attenuation is observed in areas with broad leaved vegetation, low humidity, and high temperature (Aylor, 1972; Wiley and Richards 1978; Martens, 1980; Catchpole and Slater, 2008). Most of the dryer ecoregions in our study are characterized by thorn scrub forests and are present in northwestern Mexico, that correspond to the dryest zones (≤220 mm; Fick and Hijmans, 2017).

Effect of ecological and historical factors in bird song variation

The mixed effects models helped us to gather information about the co-ocurrence of factors driving evolution of songs in islands by analyzing the response of one variable to other factors and/or their interactions (Zuur et al., 2009). Our results suggested that the best model to explain bird song differences is by bill morphology, environmental conditions, the interaction between bill morphology and environmental conditions, the genetic group, and the habitat type for each recording. This finding is interesting because our previous results showed that three of the four species have differences in bill size and environmental conditions (see above).

Our previous approaches suggested that the differences in ecological features such as environmental conditions and habitat type are affecting bird song differences between TMA and mainland populations, this could be by directly affecting sound transmission performance (Morton, 1975; Bryan and Brenowitz, 1985; Slabbekoorn and Smith, 2002) or indirectly as a result of morphological differences (Podos, 2001; Huber and Podos, 2006). However, genetic F_{ST} values and syllable sharing index are evidence of low cultural and genetic flow between TMA and mainland. Thus, the isolation of TMA populations is also an important factor that contributed to bird song divergence in these islands. This phenomenon could be easily understood in the framework of the “acoustic window”. This approach suggests that a reduction in the favorable acoustic parameters for sound transmission, given the multidimensional axis in the different habitat types, and the morphological and physiological traits, are contributing to population adaptation and divergence (Wilkins et al., 2013). Due to a reduction in biological diversity, the acoustic space available for recent colonizers could be shifted or higher than in mainland (Marler 1960), leading to an initial release of bird song constraints that was limited by their own morphology and physiology, the habitat and sexual selection (Morinay et al., 2013).

Natural and sexual selection could also be acting and selecting individuals with longer bills, what constrains the acoustic versatility as was observed in other passerine birds (Maluridae) in Australia and New Guinea (Greig et al., 2013). Our finding in syllable repertoires reduction and morphology of bill and body size, along with previous genetic studies, suggest a colonization event of a small number of individuals to TMA. Apparently those colonizers are under ecological pressures which are driving morphological and vocal traits. These findings coincide with other studies where genetic variation is closely related with acoustic differentiation (McCracken and Sheldon 1997; Price and Lanyon 2004; Päckert et al., 2013). Although we did not analyze the genes that are directly responsible of bill morphology (Wu et al., 2004, 2006; Lamichhaney et al., 2015; Cheng et al., 2017), we do not discard a possible divergence in those genes as a result of character displacement (Lamichhaney et al., 2016).

Some authors suggested that once populations got established, cultural features like bird songs could be stable for long periods of time (Pipek et al., 2018; Aplin, 2019). However, sexual selection in islands is often less intense in islands than mainland due to lower fitness benefits and low genetic variation among individuals (Griffith, 2000; Frankham, 1997) and the absence of predators, which is also reduced in islands (Beauchamp, 2004), favors the signal evolution within the acoustic window for each species. Genetic evidence suggests that TMA populations have been isolated for thousands of years. Thus, the combination of time since colonization event, founder effect, ecological differences, low migration rates, and probably lower sexual selection, have resulted in genetic and acoustic divergences between TMA and mainland. Apparently, the isolation of TMA since late Pleistocene has been favoring the fixation of different traits in TMA populations that are evolving independently from mainland.

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Figures and figure legends

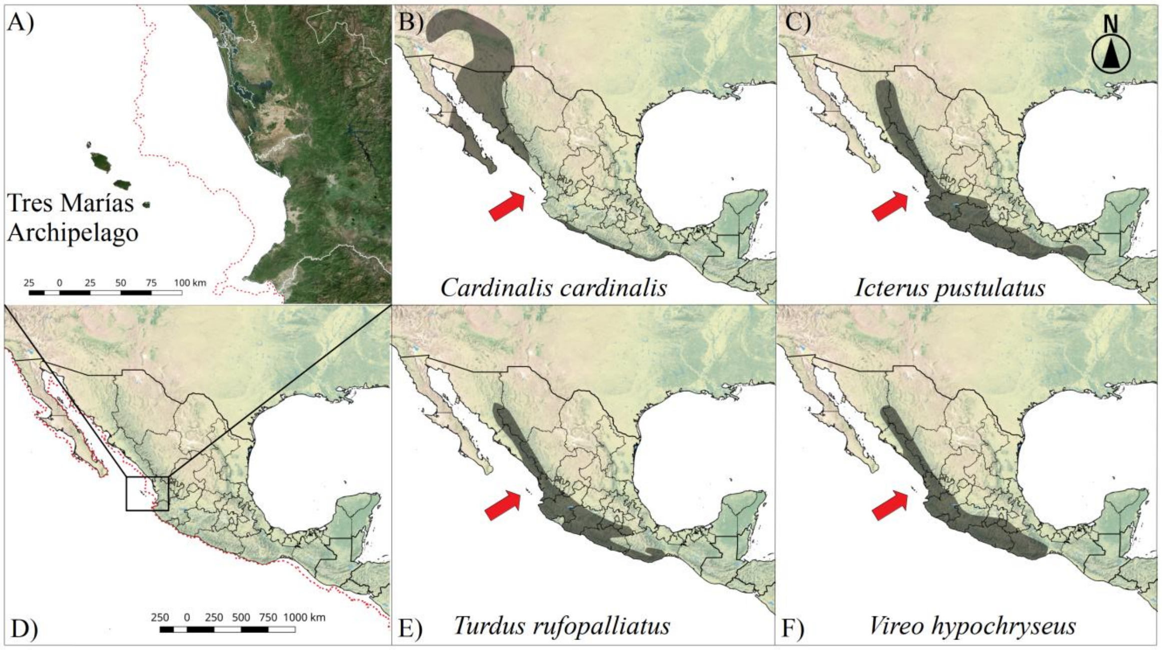
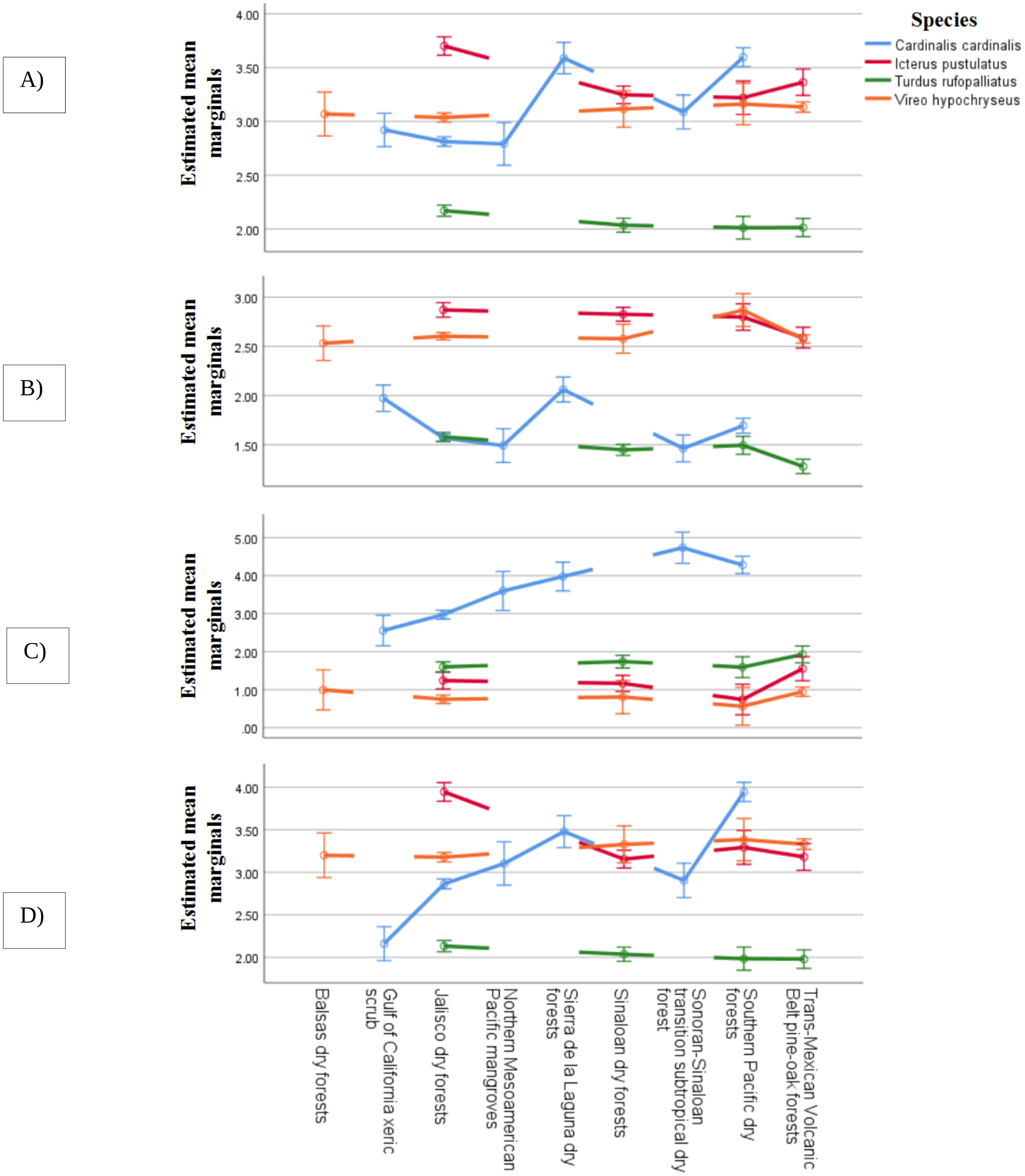


Figure 1. A and D) Map of the Tres Marías Archipelago and current geographic distance from mainland, red dashed line depicts shoreline at sea level 100m below actual sea level; B) geographic distribution of *Cardinalis cardinalis* in western Mexico; C) geographic distribution of *Icterus pustulatus* in western Mexico; E) geographic distribution of *Turdus rufopalliatus*; F) geographic distribution of *Vireo hypochryseus*; red arrows indicate that distribution include Tres Marías Archipelago.

Figure 2. Effect of habitat type in bird song frequencies of the four species. Mean marginal estimates in a Two-way ANOVA using WWF ecoregions (Olson et al. 2001) as a proxy of habitat type for each recording. A) mean dominant frequency; B) minimum dominant frequency; C) dominant frequency range; D) and mean peak of dominant frequency.



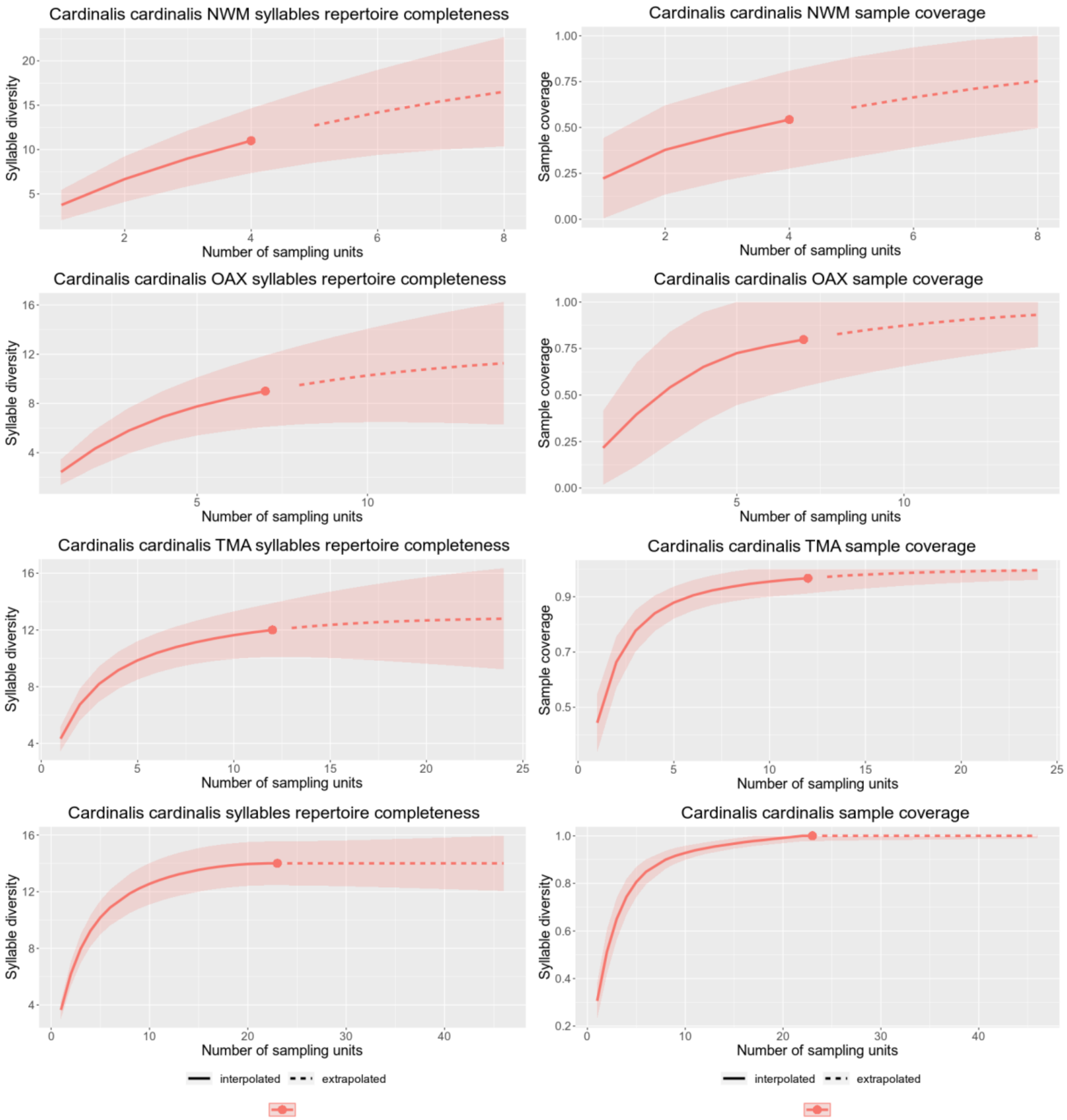


Figure 3. Accumulation curves for syllable diversity and sample completeness estimates for each genetic group and whole distribution of *Cardinalis cardinalis*.

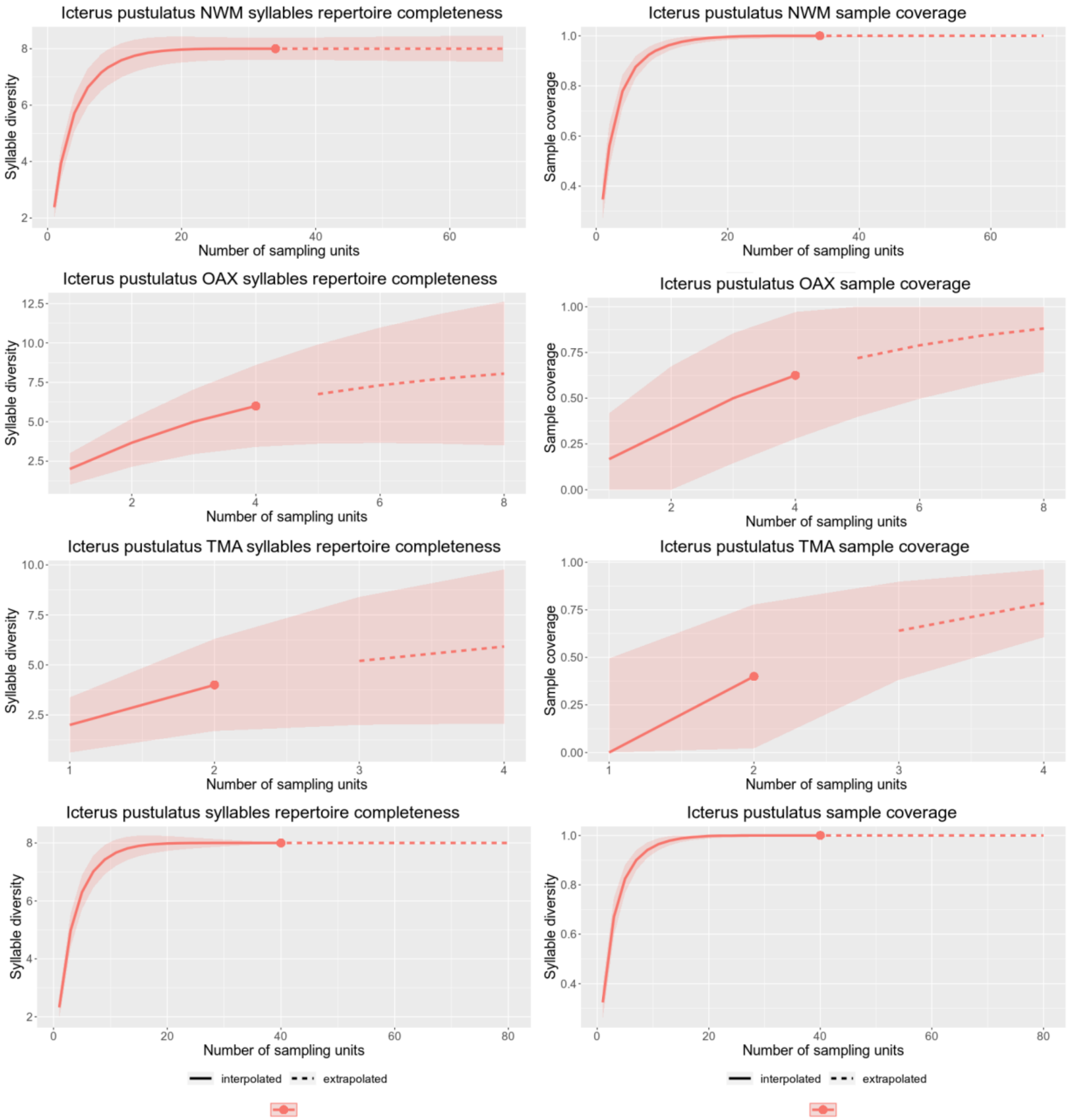


Figure 4. Accumulation curves for syllable diversity and sample completeness estimates for each genetic group and whole distribution of *Icterus pustulatus*.

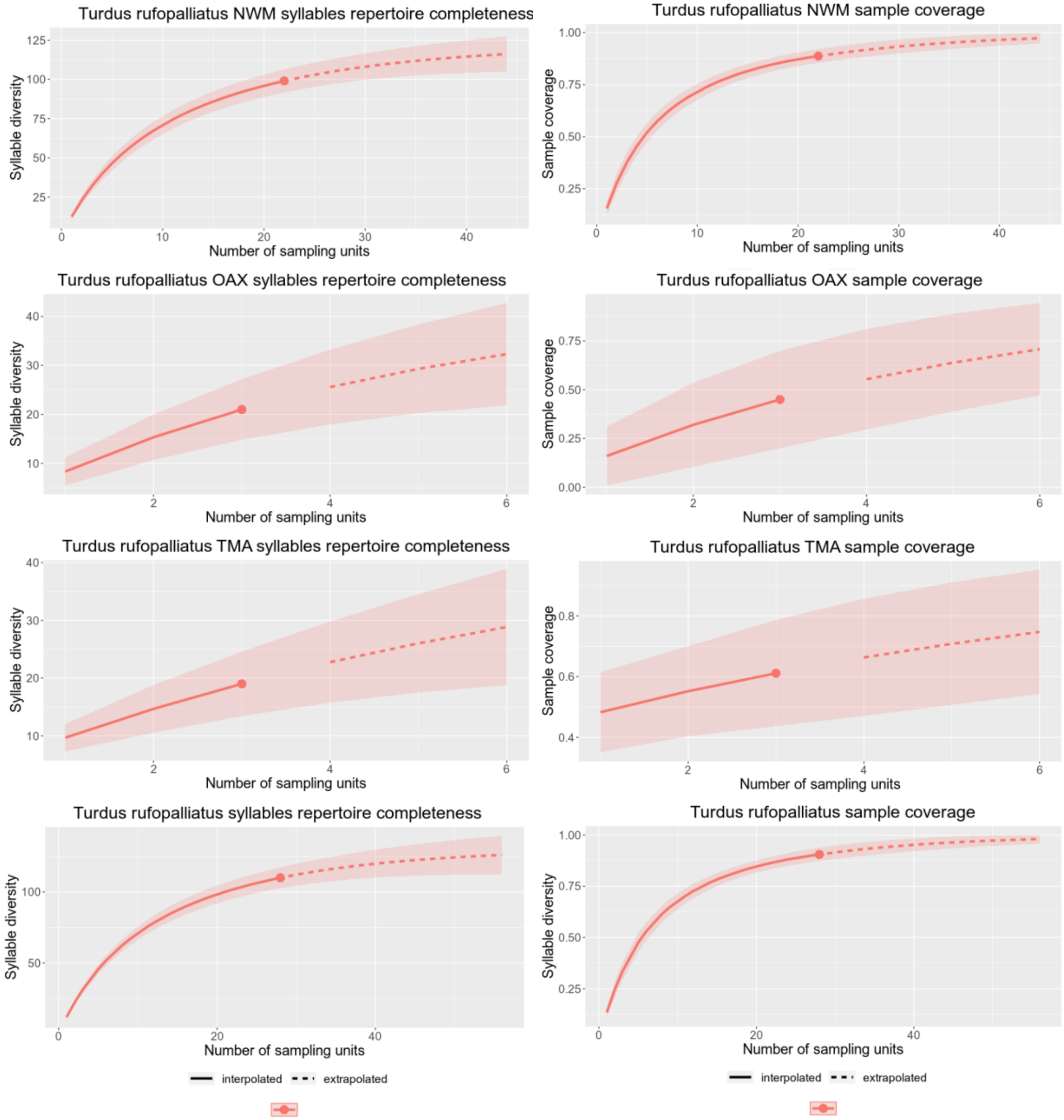


Figure 5. Accumulation curves for syllable diversity and sample completeness estimates for each genetic group and whole distribution of *Turdus rufopalliatus*.

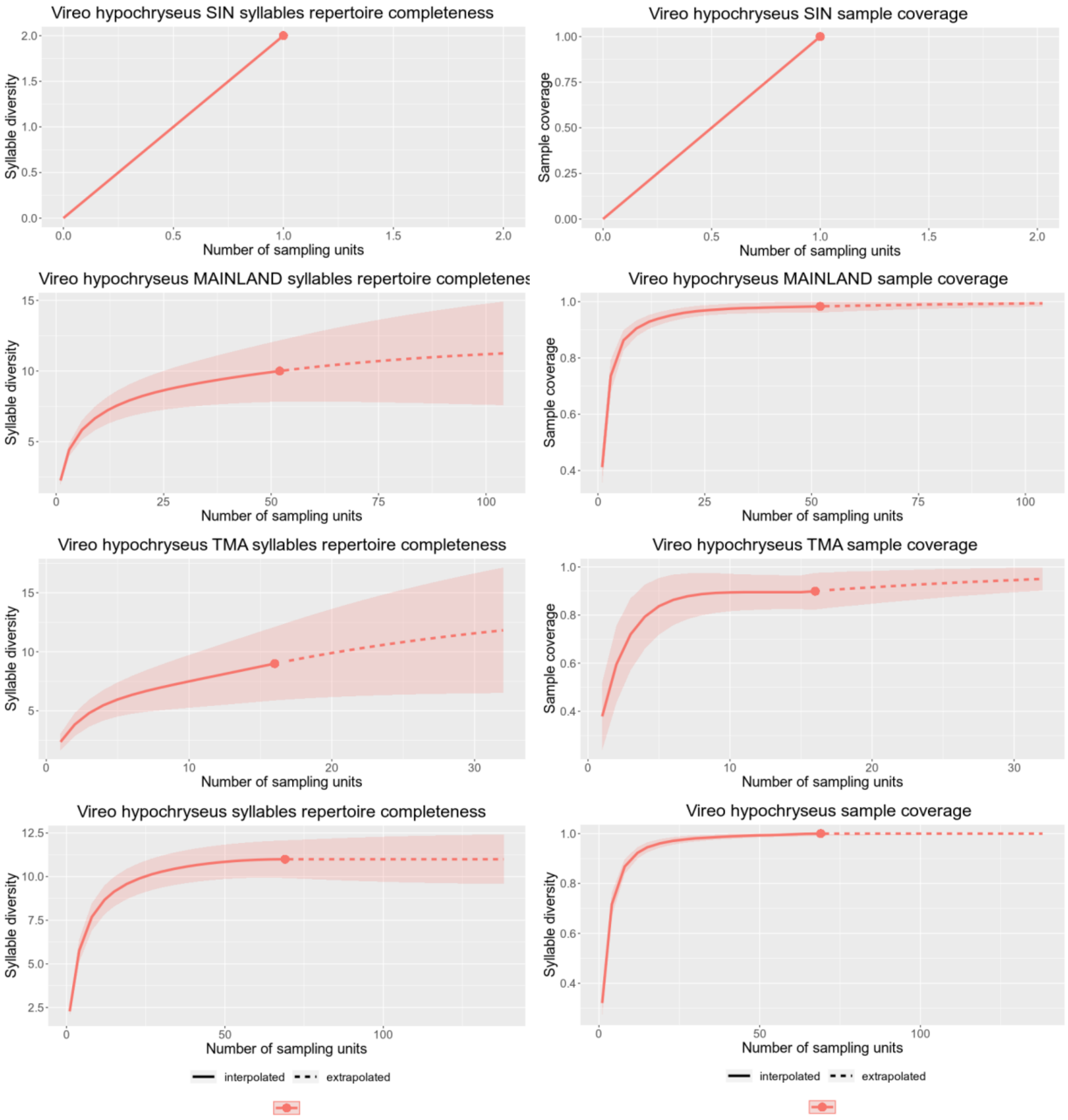


Figure 6. Accumulation curves for syllable diversity and sample completeness estimates for each genetic group and whole distribution of *Vireo hypochryseus*.

Table 1. Bill volume comparisons among genetic groups of the four species. α=0.05, significant values are depicted in boldface.

Species	**Gl**	**P value**
Cardinalis cardinalis	2	**0.001**
Icterus pustulatus	3	**<0.001**
Turdus rufopalliatus	2	**0.001**
Vireo hypochryseus	2	0.437

Table 2. Pairwise comparisons of bill volume among genetic groups of the four species. α=0.05. TMA: Tres Marías Archipelago; NWM: Northwestern Mexico (states of Sonora, Sinaloa, Nayarit and Jalisco); GRO+OAX: states of Guerrero and Oaxaca; GRO: Guerrero; OAX: Oaxaca; SIN: Sinaloa; MAINLAND: All continental populations. For *Vireo hypocrhyseus* mainland means all continental populations except Sinaloa. Significant values are depicted in boldface, α=0.05.

Species	**Genetic group**	**TMA**	**NWM**	**GRO+OAX**	**GRO**	**OAX**	**SIN**	**MAINLAND**
Cardinalis cardinalis	**TMA**	-	**<0.001**	**<0.001**	-	-	-	-
	NWM	**<0.001**	-	**<0.001**	-	-	-	-
	GRO+OAX	**<0.001**	1.000	**<0.001**	-	-	-	-
Icterus pustulatus	**TMA**	-	0.783	-	0.165	0.611	-	-
	NWM	0.783	-	-	**<0.001**	0.433	-	-
	GRO	0.165	**<0.001**	-	-	0.999	-	-
	OAX	0.611	0.433	-	0.999	-	-	-
Turdus rufopalliatus	**TMA**	-	**0.014**	**0.046**	-	-	-	**0.006**
	NWM	**0.014**	-	**0.009**	-	-	-	-
	GRO+OAX	**0.046**	**0.009**	-	-	-	-	-
	MAINLAND	**0.006**	-	-	-	-	-	-
Vireo hypochryseus	**TMA**	-	-	-	-	-	0.654	0.440
	SIN	0.654	-	-	-	-	-	0.985
	MAINLAND	0.440	-	-	-	-	0.985	-

Table 3. Repertoire sizes of the genetic groups for each species. TMA: Tres Marías Archipelago; NWM: Northwestern Mexico (states of Sonora, Sinaloa, Nayarit and Jalisco); OAX: Oaxaca; SIN: Sinaloa; MAINLAND: All continental populations. For *Vireo hypocrhyseus* mainland means all continental populations except Sinaloa.

Species	**Genetic group**					**Total syllable diversity**
	TMA	**NWM**	**OAX**	**SIN**	**MAINLAND**	
Cardinalis cardinalis	12	11	9	-	12	14
Icterus pustulatus	4	8	6	-	8	8
Turdus rufopalliatus	19	99	34	-	99	99
Vireo hypochryseus	9	-	-	2	10	11

Table 4. Repertoire sizes of the geographic areas for each species. TMA: Tres Marías Archipelago; BCS: Baja California Sur; SON: Sonora; SIN: Sinaloa; Nay: Nayarit; Jal: Jalisco; GRO: Guerrero; OAX: Oaxaca.

Species	**Geographic areas**								**Total syllable diversity**
	TMA	**BCS**	**SON**	**SIN**	**NAY**	**JAL**	**GRO**	**OAX**	
Cardinalis cardinalis	12	6	-	4	-	-	-	9	14
Icterus pustulatus	4	-	3	2	6	4	-	6	8
Turdus rufopalliatus	19	-	-	-	57	79	-	34	86
Vireo hypochryseus	9	-	-	2	4	8	1	3	11

Table 5. Syllable sharing between TMA and mainland, and among genetic groups of the four species according to Dice similarity index.

Comparisons / Species	*Cardinalis cardinalis*	*Icterus pustulatus*	*Turdus rufopalliatus*	*Vireo hypochryseus*
MAINLAND-TMA	0.83	0.67	0.32	0.84
TMA-NWM	0.78	0.67	0.32	0.36
TMA-OAX	0.76	0.40	0.72	NA
NWM-OAX	0.80	0.86	0.51	NA

Table 6. Environmental hypervolume comparisons among the genetic groups for each species. TMA: Tres Marías Archipelago; NWM: Northwestern Mexico (states of Sonora, Sinaloa, Nayarit and Jalisco); GRO+OAX: states of Guerrero and Oaxaca; GRO: Guerrero; OAX: Oaxaca; SIN: Sinaloa; MAINLAND: All continental populations. For *Vireo hypocrhyseus* mainland means all continental populations except Sinaloa. Bonferroni correction p value=0.017. Significant values are depicted in boldface α=0.05.

Species	Genetic group	TMA	NWM	OAX	SIN	MAINLAND
Cardinalis cardinalis	**TMA**	-	0.018	0.162	-	-
	NWM	0.018	-	-	-	-
	OAX	0.162	**0.003**	-	-	-
Icterus pustulatus	**TMA**	-	**0.000**	**0.000**	-	-
	NWM	**0.000**	-	-	-	-
	OAX	**0.000**	-	-	-	-
Turdus rufopalliatus	**TMA**	-	**0.002**	0.314	-	
	NWM	**0.002**	-	**<0.001**	-	-
	OAX	0.314	**<0.001**	-	-	-
Vireo hypochryseus	**TMA**	-	-	-	0.509	0.201
	SIN	0.509	-	-	-	0.722
	MAINLAND	0.201	-	-	0.722	-

Table 7. Correlation (Speraman's rho) between morphological measurements and bird song frequencies. Significant values are depicted in boldface. α=0.05.

Species	Acoustic variable	Morphometric variable	Sperman's rho	P-value
Cardinalis cardinalis	Dominant frequency mean	Weight	-0.070	0.078
		Bill size adjusted by weight	-0.350	**<0.001**
	Dominant frequency minimum	Weight	0.09	**0.015**
		Bill size adjusted by weight	-0.142	**<0.001**
	Mean peak frequency	Weight	-0.240	**<0.001**
		Bill size adjusted by weight	-0.191	**<0.001**
	Dominant frequency range	Weight	-0.054	0.167
		Bill size adjusted by weight	-0.306	**<0.001**
	Hypervolume	Weight	-0.228	**<0.001**
		Bill size adjusted by weight	0.064	0.107
Icterus pustulatus	Dominant frequency mean	Weight	-0.070	0.224
		Bill size adjusted by weight	0.070	0.224
	Dominant frequency minimum	Weight	-0.057	0.325
		Bill size adjusted by weight	0.057	0.325
	Mean peak frequency	Weight	-0.052	0.369
		Bill size adjusted by weight	0.052	0.369
	Dominant frequency range	Weight	-0.215	**<0.001**

		Bill size adjusted by weight	0.215	**<0.001**
	Hypervolume	Weight	-0.237	**<0.001**
		Bill size adjusted by weight	0.237	**<0.001**
Turdus rufopalliatus	Dominant frequency mean	Weight	-0.159	**<0.001**
		Bill size adjusted by weight	0.149	**<0.001**
	Dominant frequency minimum	Weight	-0.043	0.295
		Bill size adjusted by weight	0.159	**<0.001**
	Mean peak frequency	Weight	-0.187	**<0.001**
		Bill size adjusted by weight	0.151	**<0.001**
	Dominant frequency range	Weight	-0.077	0.059
		Bill size adjusted by weight	-0.006	0.869
	Hypervolume	Weight	-0.281	**<0.001**
		Bill size adjusted by weight	0.284	**<0.001**
Vireo hypochryseus	Dominant frequency mean	Weight	0.323	**<0.001**
		Bill size adjusted by weight	-0.323	**<0.001**
	Dominant frequency minimum	Weight	-0.110	**0.002**
		Bill size adjusted by weight	0.110	**0.002**
	Mean peak frequency	Weight	0.424	**<0.001**
		Bill size adjusted by weight	-0.424	**<0.001**
	Dominant frequency range	Weight	0.482	**<0.001**

	Bill size adjusted by weight	-0.482	**<0.001**
Hypervolume	Weight	0.123	**<0.001**
	Bill size adjusted by weight	-0.123	**<0.001**

Table 8. Relationship between bird song frequencies, ecoregions (as a proxy of habitat type) and the interaction of ecoregion and species. Significant values are depicted in boldface α=0.05.

Dependent variable	**Origin**		**Type III error square sum**	**d.f.**	**Cuadratic mean**	**F**	**p**
Mean dominant frequency	Intercept	Hypothesis	4749.048	1	4749.048	67.074	**0.004**
		Error	208.858	2.950	70.803		
	ecoregion	Hypothesis	12.173	8	1.522	0.402	0.889
		Error	27.873	7.357	3.788		
	species	Hypothesis	384.213	3	128.071	22.229	**0.001**
		Error	40.859	7.092	5.761		
	ecoregion * species	Hypothesis	49.620	7	7.089	36.422	**0.000**
		Error	444.325	2283	0.195		
Minimum dominant frequency	Intercept	Hypothesis	2521.054	1	2521.054	35.768	**0.009**
		Error	211.342	2.998	70.483		
	ecoregion	Hypothesis	18.159	8	2.270	3.931	**0.028**
		Error	5.225	9.050	0.577		
	species	Hypothesis	379.374	3	126.458	155.257	**0.000**
		Error	6.114	7.507	0.815		
	ecoregion * species	Hypothesis	6.818	7	0.974	6.701	**0.000**
		Error	331.871	2283	0.145		
Dominant frequency range	Intercept	Hypothesis	2131.510	1	2131.510	11.122	**0.045**
		Error	570.556	2.977	191.651		
	ecoregion	Hypothesis	122.807	8	15.351	1.876	0.193
		Error	67.101	8.199	8.184		

	species	Hypothesis	1035.250	3	345.083	28.845	**0.000**
		Error	87.359	7.302	11.963		
	ecoregion * species	Hypothesis	101.540	7	14.506	11.161	**0.000**
		Error	2967.139	2283	1.300		
Mean peak of dominant frequency	Intercept	Hypothesis	4692.059	1	4692.059	54.642	**0.006**
		Error	250.044	2.912	85.868		
	ecoregion	Hypothesis	54.095	8	6.762	0.866	0.581
		Error	56.887	7.283	7.811		
	species	Hypothesis	468.974	3	156.325	13.111	**0.003**
		Error	84.330	7.073	11.923		
	ecoregion * species	Hypothesis	102.823	7	14.689	45.838	**0.000**
		Error	731.594	2283	0.320		

Table 9. Mixed effects models considered to explain the acoustic variation among the four species.

Model	Fixed effect	Random effect	Grouping	Difference in AIC	d.f.
M1	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume +species+latitude	none	none	284.2	35
M2	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume+latitude	species	none	291.2	33
M3	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume+latitude	Genetic group	species	58.4	53
M4	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume+genetic group	species	latitude	0	20
M5*	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume	species	latitude	25.4	15
M6	Bill volume+environmental hypervolume+interaction between bill volume+environmental hypervolume+specie	species	none	659.3	9

*: Depicts the model with the best AIC value with significant effects.

Appendix I. Sound library sources, localities and geographic coordinates for each recording of the four species analyzed. ML: Macaulay Libray (Cornell Laboratory of Ornithology), MZFC: Biblioteca de Sonidos Naturales MZFC.

Catalog number	**Scientific name**	**Locality**	**State**	**Source**	**Latitude**	**Longitude**
16810_44k	*Cardinalis cardinalis*	3.0 km E of Altata	Sinaloa	ML	24.652467	-107.90501
16812_44k	*Cardinalis cardinalis*	192.0 km S of Guaymas	Sonora	ML	27.112493	-109.44537
16813_44k	*Cardinalis cardinalis*	19.0 km E of San Antonio	Baja California Sur	ML	23.761121	-109.91848
16814_44k	*Cardinalis cardinalis*	Concepcion bay	Baja California Sur	ML	24.075136	-110.30095
20140712_070500	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.762201	-96.186805
2020	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
2030	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
2065	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
2080	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.629028	-106.59047
2085	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.629028	-106.59047
2089	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	MZFC	21.629028	-106.59047
MO-1983	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MO-1986	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MO-1995	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MO-1996	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MO-1997	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MO-1998	*Cardinalis cardinalis*	Huatulco	Oaxaca	MZFC	15.769675	-96.194503
MZ000045	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MZ000054	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MZ000071	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MZ000072	*Cardinalis cardinalis*	Tras Marías	Nayarit	ML	21.629028	-106.59047

		Archipelago				
MZ000077	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MZ000089	*Cardinalis cardinalis*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
080101-000	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
109152_44k	*Icterus pustulatus*	5.0 km W of Alamos, Aduana Wash	Sonora	ML	27.043464	-108.99186
109153_44k	*Icterus pustulatus*	5.0 km W of Alamos, Aduana Wash	Sonora	ML	27.043464	-108.99186
109157_44k	*Icterus pustulatus*	12.0 km SE of Alamos, near Cuchujaqui River	Sonora	ML	26.924504	-108.91766
109161_44k	*Icterus pustulatus*	13.0 km SE of Alamos, near Cuchujaqui River	Sonora	ML	26.924504	-108.91766
12555_44k	*Icterus pustulatus*	44.0 km W of Tehuantepec	Oaxaca	ML	16.405016	-95.584243
12556_44k	*Icterus pustulatus*	23.0 km E of Villa Union	Sinaloa	ML	23.062383	-106.00099
12558_44k	*Icterus pustulatus*	83.0 km NW of Tehuantepec	Oaxaca	ML	16.475875	-95.885761
20140502_073426	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140502_075000	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140502_083000	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140502_085000	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140502_091000	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140517_193000	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
20140518_084700	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
20140518_085000	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
20140518_103000	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
20140519_071000	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
20140710_070500	*Icterus pustulatus*	Huatulco	Oaxaca	MZFC	15.762201	-96.186805
20140710_073000	*Icterus pustulatus*	Huatulco	Oaxaca	MZFC	15.762201	-96.186805
BRCF14_1305	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1330	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1331	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1333	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1346	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139

BRCF14_1363	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1364	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1365	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1366	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1368	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1714	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1721	*Icterus pustulatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1749	*Icterus pustulatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1788	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1789	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1790	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1812	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1820	*Icterus pustulatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-2146	*Icterus pustulatus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MPS059	*Icterus pustulatus*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
080101-000	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140429_184854	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
20140502_091000	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
20140704_091000	*Turdus rufopalliatus*	Chacahua	Oaxaca	MZFC	16.010921	-97.766334
BRCF14_1334	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1346	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1347	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1366	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1731	*Turdus rufopalliatus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1733	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1735	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1741	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1742	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1745	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1747	*Turdus rufopalliatus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1777	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1786	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1787	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1791	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1792	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431

MO-1825	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1827	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1828	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1833	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1834	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1836	*Turdus rufopalliatus*	Salazares	Nayarit	MZFC	21.677417	-104.97431
MO-1968	*Turdus rufopalliatus*	Chacahua	Oaxaca	MZFC	16.013724	-97.765924
MO-1978	*Turdus rufopalliatus*	Chacahua	Oaxaca	MZFC	16.013724	-97.765924
MO-1979	*Turdus rufopalliatus*	Chacahua	Oaxaca	MZFC	16.013724	-97.765924
MO-1982	*Turdus rufopalliatus*	Chacahua	Oaxaca	MZFC	16.013724	-97.765924
MPS212-215	*Turdus rufopalliatus*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MPS217-219	*Turdus rufopalliatus*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
MPS222-227	*Turdus rufopalliatus*	Tras Marías Archipelago	Nayarit	ML	21.629028	-106.59047
109201_44k	*Vireo hypochryseus*	56 km NE de Mazatlan Panuco Road	Sinaloa	ML	23.707743	-106.59806
109223_44k	*Vireo hypochryseus*	15.0 km W of Tepic, Cerro de San Juan	Nayarit	ML	21.593524	-104.99864
11811_44k	*Vireo hypochryseus*	8.0 km N of Chilpancingo	Guerrero	ML	17.618096	-99.518889
135519_44k	*Vireo hypochryseus*	Near El Tuito Rancho Primavera	Jalisco	ML	20.33806	-105.34541
140427-022	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140427-022	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140427-025	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140427-025	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140427-025	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-015	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-015	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-015	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-016	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-016	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140428-016	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-001	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-001	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914

140429-001	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-003	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-003	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-003	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-005	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-005	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-005	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-009	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-009	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-009	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-011	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-011	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
140429-011	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
20140502_083000	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
2022	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
2052	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
2055	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
53712_44k	*Vireo hypochryseus*	San Blas	Nayarit	ML	21.53906	-105.27402
57715_44k	*Vireo hypochryseus*	1.0 km W of Cd. Oaxaca (ruins Of Monte Alban)	Oaxaca	ML	17.04711	-96.766628
BRCF14_1302	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1302	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1305	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1305	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1305	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1318	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1318	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1318	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1331	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
BRCF14_1355	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1355	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1355	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1359	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139

BRCF14_1359	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1368	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1368	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
BRCF14_1368	*Vireo hypochryseus*	Autlan	Jalisco	MZFC	19.813894	-104.41139
MO-1721	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1721	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1721	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1722	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1722	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1722	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1724	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1724	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1724	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1725	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1725	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-1725	*Vireo hypochryseus*	Bioto	Jalisco	MZFC	20.296096	-105.36914
MO-2117	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2121	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2122	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2134	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2137	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2139	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2142	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2166	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2167	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2168	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2169	*Vireo hypochryseus*	Tras Marías	Nayarit	MZFC	21.463503	-106.42844

		Archipelago				
MO-2174	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.463503	-106.42844
MO-2185	*Vireo hypochryseus*	Tras Marías Archipelago	Nayarit	MZFC	21.324968	-106.2275

Appendix II. Description and units of the acoustic parameters measured with warbleR. Variables are grouped in three modules: 1) duration; 2) frequency, and 3) Shape of notes (roundness, flatness or peak shape).

Module	Variable	Description (units)
Duration	duration*	Length of signal (s)
	Median time	The time at which the signal is divided in two time intervals of equal energy (s)
	First quartile time	The time at which the signal is divided in two time intervals of 25% and 75% energy respectively (s)
	Third quartile time	The time at which the signal is divided in two time intervals of 75% and 25% energy respectively (s)
	Interquartile time range	Time range between first quartile time and third quartile time (s)
Frequency	Mean frequency	Weighted average of frequency by amplitude (kHz)
	Median frequency	The frequency at which the signal is divided in two frequency intervals of equal energy (in kHz)
	First quartile frequency	The frequency at which the signal is divided in two frequency intervals of 25% and 75% energy respectively (kHz)
	Third quartile frequency	The frequency at which the signal is divided in two frequency intervals of 75% and 25% energy respectively (kHz)
	Interquartile frequency range	Frequency range between first quartile frequency and third quartile frequency (kHz)
	Fundamental frequency mean*	Average of fundamental frequency measured across the acoustic signal (kHz)
	Fundamental frequency minimum*	Minimum fundamental frequency measured across the acoustic signal (kHz)
	Fundamental frequency maximum*	Maximum fundamental frequency measured across the acoustic signal (kHz)

	Dominant frequency mean	Average of dominant frequency measured across the acoustic signal (kHz)
	Dominant frequency minimum	Minimum of dominant frequency measured across the acoustic signal (kHz)
	Dominant frequency maximum	Maximum of dominant frequency measured across the acoustic signal (kHz)
	Dominant frequency range	Range of dominant frequency measured across the acoustic signal (kHz)
	Start dominant frequency*	Dominant frequency measurement at the start of the signal (kHz)
	End dominant frequency*	Dominant frequency measurement at the end of the signal (kHz)
	Dominant frequency slope	Slope of the change in dominant frequency through time ((end dominant frequency-start dominant frequency)/duration). (kHz/s)
	Mean peak frequency*	Frequency with highest energy from the mean frequency spectrum (kHz)
Shape	Skewness	Asymmetry of the frequency spectrum. S < 0 when the spectrum is skewed to left; S = 0 when the spectrum is symetric; S > 0 when the spectrum is skewed to right
	Kurtosis	Peakedness of the spectrum. K < 3 when the spectrum curve is platikurtic, i.e. it has fewer items at the center and at the tails than the normal curve but has more items in the shoulders; K = 3 when the spectrum shows a normal shape; K > 3 when the spectrum curve is leptokurtic, i.e. it has more items near the center and at the tails, with fewer items in the shoulders relative to normal distribution with the same mean and variance
	Spectral entropy	Energy distribution of the frequency spectrum. Pure tone ~ 0; noisy ~ 1
	Time entropy	Energy distribution on the time envelope. Pure tone ~ 0; noisy ~ 1
	Spectral entropy	Product of time and spectral entropy spectral entropy x time entropy
	Spectral flatness*	Estimate of the flatness of a frequency spectrum. Pure tone ~ 0; noisy ~ 1

Modulation index*	Calculated as the cumulative absolute difference between adjacent measurements of dominant frequencies divided by the dominant frequency range. 1 means the signals is not modulated

DISCUSIÓN Y CONCLUSIONES GENERALES

Discusión y conclusiones generales

El aislamiento de las poblaciones en las Islas Tres Marías generado por los cambios climáticos ocurridos durante las glaciaciones del Pleistoceno, ocasionó una reducción en el flujo genético y cultural. Lo cual, aunado al tiempo que han permanecido aisladas las poblaciones de las Islas Tres Marías, han favorecido la diferencia entre las poblaciones del oeste de México y las islas Tres Marías en caracteres genéticos, morfológicos y conductuales, particularmente en el canto de los machos. Los resultados mostraron que la colonización de las Islas Tres Marías ocurrió hace aproximadamente 120 mil años cuando las condiciones climáticas durante la glaciación provocaron una disminución en el nivel del mar reduciendo la distancia que existe entre la costa de Nayarit y las Islas Tres Marías a unos 25-30 km (McCloy et al., 1988; Zweifel 1960). Posteriormente, al terminar la glaciación los niveles del mar se elevaron al derretirse los casquetes polares y separando las islas y el continente por una distancia de ~95 km. Mis datos sugieren que la colonización de las islas ocurrió de manera simultánea por individuos provenientes del noroeste de México (Sonora, Sinaloa, Nayarit y Jalisco). Desde hace 120 mil años cuando emergieron las islas (McCloy et al., 1988), y desde entonces, las poblaciones de las islas han generado diferencias en la forma del pico, sobre todo en la longitud de los mismos. Es probable que el mayor tamaño de los picos en las islas se debida a las condiciones de temperatura y menor disponibilidad de agua dulce que favorecen la pérdida de calor a través de la superficie del pico (Tattersall et al., 2009; Greenberg et al., 2012; Greenberg y Danner 2013).

Los análisis genéticos y del tamaño de repertorio no mostraron evidencia de altos niveles de flujo génico y cultural entre las islas y el continente. De hecho, se observó una reducción en el tamaño del repertorio vocal que concuerda con lo esperado por el efecto fundador (Baker y Jenkins 1987). A pesar de que en algunas especies se ha observado un incremento en el tamaño del repertorio vocal en islas (Kroodsma et al., 1999; Baker et al., 2003), sólo en *Cardinalis cardinalis* podría existir este patrón. Sin embargo, no hay certeza en el tamaño de repertorio de dicha especie en la muestra del continente y no es un resultado robusto, dado que los tamaños de repertorio observados en otras poblaciones continentales son muy similares e incluso ligeramente mayores (Lemon 1965). Cabe señalar que el esfuerzo de muestreo en varios casos es insuficiente a pesar de ser lo que se empleó lo que está disponible a nivel mundial en la actualidad. Esto muestra que aún hace falta mucho trabajo de campo en el estudio de las aves.

Las condiciones climáticas entre las islas y el continente difieren ligeramente (Grant 1971), sin embargo, los resultados muestran que las condiciones ambientales en las que se encuentra *Vireo hypochryseus* no difieren de las condiciones en las que se encuentran en el continente. Considerando que ésta especie a pesar de que se distribuye a lo largo de la vertiente del Pacífico mexicano, durante el trabajo de campo, observé que se encuentran con mayor frecuencia en las zonas de ecotono entre bosque de encino y bosque tropical caducifolio, mientras que en las islas se ubican en zonas con mayor humedad como los bosques de galería (observación personal). Esto sugiere que las condiciones de temperatura y humedad entre el bosque tropical caducifolio y el bosque de galería son más parecidas entre sí que con las de bosque tropical caducifolio de las islas Tres Marías. Aparentemente, dichas condiciones no han afectado la morfología su pico y tampoco sus cantos.

En varios estudios se ha observado que en diversas especies las características del tamaño y forma del pico son muy plásticas y que pueden cambiar en la población en periodos relativamente cortos de tiempo, ya sea debido a cambios en el clima o a las interacciones ecológicas (Cheng et al. 2017; Grant y Grant 2017; Grant 2006). A pesar de no haber encontrado relación entre la diferencia genética y los cantos de las aves estudiadas, diversos estudios han mostrado que la expresión de diferentes genes están relacionados al tamaño y forma del pico (Lamichhaney et al., 2015; Lamichhaney et al., 2016). Nuestros análisis filogenéticos fueron realizados utilizando marcadores moleculares de DNA mitocondrial (ND2 y CytB), mismos que son muy buenos para resolver relaciones filogenéticas entre especies y en ocasiones poblaciones. Sin embargo, el uso de marcadores directamente relacionados con la forma y tamaño del pico como BMP4, CALM1, DKK3 FGF8 entre otros (Abzhanov et al. 2006; Abzhanov et al. 2004; Abzhanov y Tabin 2004; Wu et al. 2004, 2006; Mallarino et al. 2011), habrían dado mejores resultados para analizar la relación que existe entre la divergencia acústica y genética.

El análisis en conjunto del aislamiento geográfico, el tiempo que han estado aisladas, la población de la cual provienen los individuos de las islas Tres Marías, las diferencias ambientales, genéticas y morfológicas han permitido concluir que la evolución de los cantos en las islas Tres Marías está siendo modelada por las diferencias ambientales y morfológicas del pico y no por las diferencias genéticas observadas entre las islas y el continente. De modo que las diferentes características que presentan las poblaciones de las islas están evolucionando de manera independiente al de las poblaciones del continente.

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