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

PATRONES FILOGEOGRÁFICOS Y CONSERVACIÓN DE UNA AVIFAUNA ALTAMENTE ENDÉMICA: LA SIERRA MADRE DEL SUR

TESIS

(POR ARTÍCULO CIENTÍFICO)
The geography of evolutionary divergence in the highly endemic avifauna from the Sierra Madre del Sur, Mexico

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA

Biól. ALBERTO ROCHA MÉNDEZ

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CD. MX. **NOVIEMBRE, 2019**

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ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
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Presente.

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **26 de agosto de 2019** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Biología Evolutiva** del alumno **ROCHA MÉNDEZ ALBERTO** con número de cuenta **309227287** por la modalidad de graduación de **tesis por artículo científico** titulado: **"The geography of evolutionary divergence in the highly endemic avifauna from the Sierra Madre del Sur, México"**, que es producto del proyecto realizado en la maestría que lleva por título "**Patrones filogeográficos y conservación de una avifauna altamente endémica: La Sierra Madre del Sur**" ambos realizados bajo la dirección del **DR. ADOLFO GERARDO NAVARRO SIGÜENZA**, quedando integrado de la siguiente manera:

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

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 4 de noviembre de 2019

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

COORDINACIÓN

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RESUMEN

Mesoamérica (México central hasta Centroamérica) es una región con una extraordinaria complejidad geológica y ecológica. Dentro del norte de Mesoamérica, la provincia biótica de la Sierra Madre del Sur (SMS) en el suroeste de México alberga una gran cantidad de diversidad y grupos endémicos de aves. En este trabajo, se han buscado patrones filogeográficos temporal y espacialmente concordantes, así mismo se han investigado sus causas a través de pruebas de hipótesis que involucran procesos históricos en cuatro géneros de aves pertenecientes a tres órdenes distintos. Las especies seleccionadas incluyen poblaciones endémicas y diferenciadas a lo largo de los bosques montanos de Mesoamérica, y particularmente aquellos que se encuentran dentro de la SMS. Se obtuvieron secuencias de al menos una región de ADN mitocondrial a partir de 177 individuos de todas las especies analizadas. Se evaluó la estructura genética, la historia demográfica y se definieron hipótesis biogeográficas para evaluar la co-varianza temporal y espacial. Los análisis sugieren cortes filogeográficos compartidos en áreas que corresponden a las poblaciones del SMS, y entre los principales sistemas montañosos en Mesoamérica, siendo el Valle central de Oaxaca y la Depresión de Nicaragua los cortes que con más frecuencia se compartieron entre los taxa analizados. A pesar de compartir este patrón geográfico, los análisis de datación de las divergencias son consistentes con una hipótesis de múltiples eventos vicariantes a lo largo de Mesoamérica derivado de mecanismos operando a distintas escalas temporales sobre los taxa en la SMS. Este estudio provee un marco de referencia para entender los orígenes evolutivos y los factores históricos que aumentan los procesos de especiación en regiones bien definidas dentro de Mesoamérica, lo cual indica que la historia evolutiva de la biota existente que habita los bosques montanos es compleja e idiosincrática.

ABSTRACT

Mesoamerica (central Mexico through Central America) is a remarkable region with a high geological and ecological complexity. Within northern Mesoamerica, the biotic province of the Sierra Madre del Sur (SMS) in southwestern Mexico harbors an exceptionally high avian endemism and diversity. Herein, we searched for spatially and temporally concordant phylogeographic patterns, and investigated their causes through hypothesis testing regarding historical processes in four bird genera from three distinct avian orders. Selected species include endemic and differentiated populations across the montane forests of Mesoamerica, and particularly within the SMS. We recovered mitochondrial DNA sequences for at least one locus from 177 individuals across all species. We assessed genetic structure, demographic history, and defined a framework for the coalescent simulations used in biogeographic hypothesis testing temporal and spatial co-variance. Our analyses suggested shared phylogeographic breaks in areas corresponding to the SMS populations, and between the main montane systems in Mesoamerica, with the Central Valley of Oaxaca and the Nicaragua Depression being the most frequently shared breaks among analyzed taxa. Nevertheless, dating analyses and divergence patterns observed were consistent with the hypothesis of broad vicariance across Mesoamerica derived from mechanisms operating at distinct times across taxa in the SMS. Our study provides a framework for understanding the evolutionary origins and historical factors enhancing speciation in well-defined regions within Mesoamerica, indicating that the evolutionary history of extant biota inhabiting montane forests is complex and often idiosyncratic.

INTRODUCCIÓN

La historia reciente de las especies puede ser comprendida cuando datos genéticos son examinados en un contexto geográfico. Por tanto, la comparación de patrones filogeográficos entre especies co-distribuidas provee de información sobre la probable congruencia de los procesos que pudieron haber conducido la diversificación inter e intraespecífica en una región en particular (Avise 2000, 2008; Hickerson *et al.,* 2007; D' Amen *et al.,* 2012). Diversos estudios filogeográficos enfocados en aves han demostrado que la estructura genética se asocia frecuentemente con áreas de distribución disyuntas, así como a barreras geográficas que restringen la mezcla entre poblaciones, lo que conlleva hacia diferenciación genética (*e. g.,* Hewitt 2000; Navarro-Sigüenza *et al.,* 2008; Barrera-Guzmán *et al.,* 2012; Navarro-Sigüenza *et al.,* 2013), y frecuentemente a la diferenciación en caracteres ecológicos y conductuales (*e. g.,* Milá *et al.,* 2009; Pérez-Emán *et al.,* 2010; Cicero y Koo, 2012; Ortíz-Ramírez *et al.,* 2016). En contraste, se han realizado relativamente pocos esfuerzos en la formulación de hipótesis robustas que busquen explicar patrones distribucionales compartidos, aun cuando se espera que las especies que comparten áreas geográficas deberían de ser influenciados por procesos históricos semejantes (Avise, 2000; Linder, 2001; Sánchez-González y Navarro-Sigüenza, 2009; Arbeláez-Cortés *et al.,* 2012, 2014a).

Mesoamérica, está situada en la región más norteña del Neotrópico, evidencia una gran cantidad de procesos de diferenciación inter e intraespecífica para distintos grupos de organismos (ver Halffter *et al.,* 2008; Carnaval *et al.,* 2009). La región posee uno de los mayores niveles de endemismo y diversidad de especies, pero también una de las biotas mayormente amenazadas así como altos niveles de deforestación (Harris *et al.,* 2000; Ornelas *et al.,* 2010). La historia geológica de Mesoamérica (*e.g.,* Formación de arcos volcánicos durante el Mioceno-Plioceno, formación del Istmo de Tehuantepec y Depresión de Nicaragua), así como sus cambios cíclicos de clima y vegetación durante el Pleistoceno, la posiciona como un área compleja y desafiante para estudios biogeográficos y evolutivos. Además, los constantes procesos orogénicos han promovido una topografía fragmentada, la cual ha promovido el desarrollo de parches aislados de bosques húmedos de montaña entre los 600 a 3000m (Hernández-Baños *et al.,* 1995; Luna-Vega *et al.,* 2016; Morales *et al.,* 2016). Estos paisajes heterogéneos tipo mosaico, han sido asociados con divisiones biogeográficas, centros de diversificación y altos niveles de endemismo y riqueza de especies en comunidades bióticas durante los últimos dos millones de años, debido a factores como la complejidad ambiental y geológica, así como a fluctuaciones climáticas ocurridas durante el Pleistoceno (Hewitt, 2000; Hernández-Baños *et al.,* 1995; García-Moreno *et al.,* 2004; Carnaval *et al.,* 2009; Ornelas *et al.,* 2010, 2013; Arbeláez-Cortés *et al.,* 2014a; Bertelli *et al.,* 2017; Antonelli *et al.*, 2018). Debido a que el endemismo no se distribuye azarosamente y posee límites dinámicos (Halffter, 1991; Pinilla-Buitrago *et al.*, 2018), estas regiones albergan números particularmente altos de especies endémicas en diversos grupos taxonómicos, incluyendo aves (González-Villareal, 2003; Campbell *et al.*, 2009; Ordóñez-Garza *et al.*, 2010; Feria-Ortíz y García-Vázquez, 2012; Navarro-Sigüenza *et al.*, 2016).

La Sierra Madre del Sur (SMS) es una provincia biogeográfica incluida en las tierras altas de Mesoamérica, y forma parte de la Zona de Transición Mexicana (ZTM, Morrone, 2015). La SMS es un sistema orográfico localizado al suroeste de México. Tiene una orientación este-oeste a lo largo de la vertiente del Pacífico (Jalisco a Oaxaca, 16-18°N, 95-102°W) con una extensión general cercana a los 56,729 km2 (Morrone, 2017). Está delimitada al este por las tierras bajas áridas del Istmo de Tehuantepec; al sur y al oeste por la vertiente del Pacífico y al norte por la cuenca del Balsas y la Faja Volcánica Transmexicana (Barrier *et al.*, 1998; Morán-Zenteno *et al.*, 1999, 2000; Ferrari *et al.*, 2012). La región alberga 622 especies de aves, de las cuales 29 (4.6%) se encuentran clasificadas como semi-endémicas, 15 (2.4%) como cuasi-endémicas y 54(8.6%) son endémicas de México. Además, 134 (21.5%) especies son consideradas bajo alguna categoría de riesgo (Navarro-Sigüenza *et al.*, 2016). Es notable que un gran número de taxones de aves en Mesoamérica son politípicos y poseen varias subespecies distribuidas a lo largo de la región (Cortés-Rodríguez *et al.*, 2008; Klicka *et al.*, 2011; Arbeláez-Cortés *et al.*, 2014b; Núñez-Zapata *et al.*, 2016; Mason *et al.*, 2018). En muchos casos, la SMS alberga subespecies endémicas y bien diferenciadas, sugiriendo la importancia del aislamiento geográfico en la evolución de variación intra-específica de sus aves (Navarro-Sigüenza y Peterson, 2004; Sánchez-González y Navarro-Sigüenza, 2009).

Los parches aislados de bosques montanos han favorecido la divergencia en poblaciones de varias especies, funcionando como modelo para la comprensión del proceso de especiación en entornos biogeograficos insulares (Masta, 2000; McCormack *et al.*, 2008; Tennessen y Zamudio, 2008; Chan *et al.*, 2011; Duennes *et al.*, 2012). Los ambientes insulares influyen en la dinámica poblacional promoviendo tamaños efectivos poblacionales reducidos (Soltis *et al.*, 2006; Qu y Lei, 2009; Qu *et al.*, 2010; Chan *et al.*, 2011; Ornelas *et al.*, 2013; Endo *et al.*, 2015; Oswald *et al.*, 2017) que pueden involucrar un menor potencial adaptativo y mayor riesgo de extinción debido a los efectos estocásticos de la deriva génica (Moritz y Faith, 1998; Pearse y Crandall, 2004; Frankham, 2010, 2014; Gamble *et al.*, 2011; Qu *et al.*, 2015; Yannic *et al.*, 2016).

En este estudio, se compararon los patrones de estructura filogeográfica entre cuatro taxones de aves no emparentados que presentan poblaciones diferenciadas y restringidas a la Sierra Madre del Sur. Se buscó determinar si la estructura filogeográfica es congruente entre taxones, y por tanto revelará patrones de diversificación simultánea. Se utilizó un conjunto de datos mitocondriales en un marco de filogeografía comparada para evaluar: a) la presencia de estructura geográfica y patrones intra-específicos de diversificación; b) la existencia de variación genética concordante entre especies; c) evaluar la potencial existencia de una historia biogeográfica y diversificación común entre especies, que soporte escenarios de vicarianza, dispersión o mezcla poblacional; y finalmente d) la importancia que distintos factores ecológicos o geológicos tuvieron para la evolución de la estructura genética en taxones que comparten las mismas barreras al flujo genético.

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The geography of evolutionary divergence in the highly endemic avifauna from the Sierra Madre del Sur, Mexico

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Abstract

Background: Mesoamerica is a remarkable region with a high geological and ecological complexity. Within northern Mesoamerica, the biotic province of the Sierra Madre del Sur (SMS) in southwestern Mexico harbors exceptionally high avian endemism and diversity. Herein, we searched for spatially and temporally concordant phylogeographic patterns, in four bird genera from three distinct avian orders co-distributed across Mesoamerica and investigated their causes through hypothesis testing regarding historical processes. Selected species include endemic and differentiated populations across the montane forests of Mesoamerica, and particularly within the SMS.

Results: We gathered mitochondrial DNA sequences for at least one locus from 177 individuals across all species. We assessed genetic structure, demographic history, and defined a framework for the coalescent simulations used in biogeographic hypothesis testing temporal and spatial co-variance. Our analyses suggested shared phylogeographic breaks in areas corresponding to the SMS populations, and between the main montane systems in Mesoamerica, with the Central Valley of Oaxaca and the Nicaragua Depression being the most frequently shared breaks among analyzed taxa. Nevertheless, dating analyses and divergence patterns observed were consistent with the hypothesis of broad vicariance across Mesoamerica derived from mechanisms operating at distinct times across taxa in the SMS.

Conclusions: Our study provides a framework for understanding the evolutionary origins and historical factors enhancing speciation in well-defined regions within Mesoamerica, indicating that the evolutionary history of extant biota inhabiting montane forests is complex and often idiosyncratic.

Keywords: Approximate Bayesian Computation, coalescent, comparative phylogeography, Mesoamerica, Mexico, montane forest, mtDNA, Pleistocene, Sierra Madre del Sur

Background

Comparison of phylogeographic patterns across co-distributed species provides valuable insights on the probable congruence of processes that may have driven intraspecific diversification in particular regions [1-4]. Several phylogeographic studies of individual bird species have shown that genetic structure is frequently associated to discontinuous ranges and geographical barriers that restrict admixture between populations, leading to genetic differentiation (see [5-8]) which may have proceeded independently or jointly with the divergence in morphological, behavioral or ecological traits (see [9-13]). However, a relatively lesser effort has been dedicated to provide robust biogeographic hypotheses seeking to explain shared distributional patterns, even when it may be expected that species sharing geographic areas should show congruent spatio-temporal patterns of differentiation [1,14-17,28,142].

Situated at the northernmost Neotropics, Mesoamerica possess one of the highest levels of endemism and species diversity, but it is also one of the most globally threatened biota and high rates of deforestation [18,19]. The complex geological history of this region, as well as the cyclic changes in vegetation and climate, pose it as a challenging area for biogeographic and evolutionary studies; in addition, constant orogenic processes have promoted a highly broken topography characterized by isolated patches of humid montane forest between 600 and 3000 m, which includes both humid pine-oak forest and cloud forest [20-22]. This mosaic-like landscape has been associated to centers of diversification, in which both a high species richness and endemism have evolved for the last 2 Myr, likely as a result of both environmental and geological complexity, as well as Pleistocene climatic fluctuations [6,15,20,23-28], which is supported by relatively recent intraspecific differentiation processes in several groups of organisms (see [25,29]), therefore explaining the existence of numerous endemic species in different taxonomic groups, including birds [30-34].

The Sierra Madre del Sur (SMS) biogeographic province is included within the Mesoamerican highlands, in the Mexican Transition Zone (MTZ, [35]). This isolated mountain range is mostly surrounded by dry lowlands of the Isthmus of Tehuantepec (IT) to the east, the Pacific slope to the south and west, the Balsas Depression and the central Trans-Mexican Volcanic Belt to the north (Figure 1; [36-39]). The SMS with an overall extension of ca. 56,729 km^2, is located along the Mexican Pacific slope (Jalisco to Oaxaca, 16-18°N, 95-102°W) [40]. The region hosts 622 avian species, 29 (4.6%) of which are classified as semi-endemic, 15 (2.4%) as quasi-endemic, and 54 (8.6%) are endemic to Mexico; in addition, 134 (21.5%) species are considered in some category of risk [33]. Furthermore, as in other Mesoamerican bird taxa [41-45], the SMS holds endemic and well-differentiated subspecies, suggesting the importance of isolation for the evolution of intraspecific variation [17,46].

Isolated montane forest patches are generally thought to act as promoters for divergence between populations of several species, which have served as models for the understanding of speciation processes in island-like settings [47-51]. These fragmented habitats influence the population dynamics and demography, given that resident populations typically show reduced effective population sizes [28,47,52-57], they are prone to a reduced adaptive potential and increased extinction risk due to the stochastic effects of genetic drift [58-64]. Therefore, the study of evolutionary history of co-distributed species in these habitats is highly important for conservation purposes.

Herein, we compared phylogeographical structure patterns among four co-distributed and not closely-related Neotropical bird taxa with well-differentiated populations restricted to the SMS. We aimed to determine whether phylogeographic structure and divergence times in each taxon are congruent among taxa, therefore revealing patterns of simultaneous diversification. Specifically, we used mitochondrial datasets in a comparative phylogeography framework to test: (1) The presence of geographically-structured genetic variation; (2) the existence of spatially-congruent genetic variation across analyzed species; (3) if biogeographic history and similar diversification scenarios support vicariance, dispersal or population admixture. In addition, we also examined temporal patterns of diversification through hABC simulations, testing for either synchronous or multiple pulses for diversification in bird assemblages across the SMS region, which allowed us to test the relative importance of ecological or geological factors linked to the evolution of the genetic structure in taxa sharing the same barriers to gene flow.

Results

Phylogenetic and population structure analyses

All of our phylogenetic and genetic assignment analyses supported previous findings on the genetic structure for all of the taxa (Figures 2, 3). Genetic structure is clearly delimited by landscape breaks corresponding to the main montane regions in Mexico and Central America. Nevertheless, we found that the detected genetic structure in these taxa is not coincident with the accepted taxonomy at the intraspecific level.

We found four distinctive lineages in *Aulacorhynchus*. Two of these, SMS (restricted to the SMS highlands) and EMx-NCA (widespread in Mesoamerica, including SMO, TM, Chiapas, and northern Central America) are differentiated by 27 mutational steps (Figure 2c). The other two are distributed in southern Central America from Costa Rica to Panama. Phylogenetic analyses support this structure with ML bootstrap values and BI posterior probabilities above 80 and 0.9 respectively (Figure 2e). We further observed two subclades in SMS samples, each representing Oaxaca and Guerrero populations.

For *Chlorospingus*, we observed six distinct mtDNA lineages, four of which included Mexican samples (Figure 2d). Individuals representing the SMS (Sierra de Miahuatlán, Oaxaca and Guerrero) were recovered in a separated group from samples from northern Oaxaca, which clustered with samples from the eastern Sierra Madre Oriental highlands (SMO); both groups are separated by 26 mutational steps. A third group corresponded to the Chimalapas (Oax.) and northern Chiapas region, while the fourth group corresponded exclusively to the TM, separated from the SMS by 32 mutations. This genetic structure is supported by BI, as well as by genetic assignment analyses with overall high posterior probabilities. Some nodes however, showed low bootstrap and posterior probability values (Figure 2f). As observed in *Aulacorhynchus*, samples from the states of Oaxaca and Guerrero were recovered as distinct subclades within the SMS.

In *Cardellina*, we found three lineages representing *C. rubra* separated by 11 to 24 mutational steps (Figure 3c). *Cardellina versicolor*, the sister species, is differentiated by more than 30 mutational steps from the *C. rubra* group. Within *C. rubra*, all recovered lineages coincide with previous findings, with one group found in the SMOc, another in the TMVB, and a third one in the SMS. We found 8 samples from a locality in central Guerrero (Carrizal de Bravo) from the SMS to be grouped in the TMVB clade, which also includes samples from localities of Jalisco and Michoacán. This paraphyletic relationship was recovered in all analyses, receiving strong support from both bootstrap (>80) and Bayesian posterior probabilities (1; Figure 3e). Nevertheless, genetic assignment analysis yielded a distinct result for these Guerrero samples, particularly for three of them (jk04-349, jk04-351, and jk04-353), which clustered with the SMS group; the remaining five clustered with the TMVB group.

Finally, in *Eupherusa-Thalurania*, we found five lineages corresponding to the currently recognized species. *T. ridgwayi* group is separated by 39 mutational steps from all of the *Eupherusa* samples; species from the SMS *E. cyanoprhys* and *E. poliocerca* haplotypes are separated by 22 mutational steps; and finally, species *E. nigriventris* and *E. eximia* are separated by 50 mutations (Figure 3d). Topologies from BI, ML (Figure 3f) recovered high posterior probabilities and bootstrap support values (> 0.8, > 75 respectively). All analyses recovered a monophyletic *Eupherusa* genus, where the SMS is represented by *E. poliocerca* and its sister species *E. cyanophrys*, and a clade from eastern Mexico to Central America, composed of *E. eximia* sister to *E. nigriventris*. Finally, for each of these species, we did not find evidence supporting further intraspecific genetic structure, even when their distribution, as in *E. poliocerca* (Oaxaca-Guerrero) and *E. eximia* (*E. e. nelsoni*, *E. e. eximia*, and *E. e. egregia*), has been described to be disjunct.

Hierarchical AMOVAs (Table 1) for the analyzed species showed that variation was explained by differences among groups. In this case, the fixation indices among groups (F_{CT}) were not significant, whereas fixation indices among populations within groups (F_{SC}) were. Genetic diversity varied among datasets. Overall, we obtained high haplotype diversity (Hd > 0.5) and low nucleotide diversity (Table 2). The only low value of Hd was observed in *E. cyanophrys*. Fu's $\mathrm{F_S}$ and Tajima's D values were not significant, excepting TMVB and SMS in *Cardellina*; however, we observed a tendency towards negative values (Table 2).

Overall, pairwise F_{ST} values showed significant high genetic differentiation between analyzed groups. However, probably due to small sample sizes, some comparisons showed no significant values, as in the SP cluster of *Aulacorhynchus* (Table 3), as well as in comparisons between *E. nigriventris* vs

T. ridgwayi, and *E. nigriventris* vs *E. cyanophrys* clusters (Table 4). The lowest F_{ST} value obtained occurred between *Cardellina* clusters from the TMVB vs SMS (Table 4).

Divergence time estimation and Coalescent-based estimation of population history

Even when divergence dates varied, analyses showed that divergence between populations occurred during the Pleistocene, mainly within the last 2 Myr. The best-supported scenario for four population groups in *Aulacorhynchus* was scenario 1(Additional file 5: Fig. 5), with a posterior probability (PP) of 0.57 and a 95% confidence interval (CI) of 0.5584 – 0.5816 (Figure 4a), which suggested that SMS, EMx-NCA, and CR-NP populations arose from an ancestral SP population, following a northwards divergence pattern. Confidence in scenario choice tested through type I and II errors, suggested the selection of a highly accurate scenario (Additional file 3). Posterior parameter estimates (Table 5) indicated that initial divergence (*t4*) from southern Panama northwards across the lowlands and narrowest region in Central America (Panama Channel Fault Zone) started during the Pliocene at 4.3 Myr (95% CI: 4 – 4.8 Myr), followed by successive northward expansion and further vicariance of populations, and the final divergence between eastern (EMx-NCA) and southwestern (SMS) Mexican populations (*t2*) about 1.3 Myr (95% CI: 420 kyr – 2.5 Myr) during the Pleistocene. When the lineages of Guerrero and Oaxaca were considered as distinct populations (Additional file 5: Fig. 6), the best scenario was scenario 2 (PP of 0.677, 95% CI: 0.668 – 0.687; Figure 4b). Type I and II errors indicated moderate confidence in the selected scenario (Additional file 3). Under this scenario, diversification patterns were similar to the latter, but the most recent divergence event occurred between Oaxaca and Guerrero populations (Additional files 4 & 5). Mean posterior parameter estimates (Table 5) indicated that the first divergence (*t4*) event is dated around 3.3 Myr (95% CI: 2.5 – 6.1 Myr), while the most recent divergence time (*t1*) occurred about 204 kyr (95% CI: 12.8 – 730 kyr).

The best scenario for *Chlorospingus* when six groups are considered (Additional file 5: Fig. 7), was scenario 1 (PP = 0.519, CI: 0.4965 – 0.5427; Figure 4c). Confidence in scenario choice was high given the values for type I and II errors (Additional file 3). This scenario suggested an initial divergence (*t6*) of Mexican and Central American lineages during the Pliocene at 5.8 Myr (95% CI: 2.5 – 9.5 Myr (Table 5), diversification of Mexican lineages proceeded westward, with the latter divergence event (*t2*) between NCA and SCA at 1.3 Myr (95% CI: 138 kyr – 2.7 Myr; Additional files 4 & 5). When lineages from Oaxaca and Guerrero were considered as distinct populations, scenario 1 (Additional file 5: Fig. 8) received the better support (PP = 0.6, 95% CI: 0.5909 – 0.625; Figure 4d), with high confidence (Additional file 3). Scenario 1 suggested diversification events similar to the latter, mean parameter estimates (Table 5) suggested an initial divergence time (*t*6) at 2 Myr (95% CI: 1.1 – 5.3 Myr) between Mexican and Central American lineages, a divergence event (*t*2) estimated to occur after the Nicaragua Depression formation between Central American populations at 1 Myr (95% CI: 288 kyr – 2.1 Myr), and a final divergence event (*t1*) in the SMS lineage originating Guerrero and Oaxaca populations during a interglacial period in the pre-Illinoian stage at 656 kyr (95% CI: 50 kyr – 1.6 Myr; Additional files 4 & 5).

Best-supported scenario in *Cardellina* was scenario 3 (PP = 0.4414, CI: 0.43 – 0.45; Figure 4g), with high confidence (Additional file 3). Scenario 3 (Additional file 5: Fig. 9) predicts an initial northward dispersal event from northern Central America (*C. versicolor*) population through the Isthmus of Tehuantepec at *t4* (~1.3 Myr); followed by vicariance events driven by the effect of Mexican highlands at *t3* (~426 kyr) between SMOc and an hypothetical ancestral population that at *t2* (~260 kyr) is fragmented into the TMVB and SMS populations (Table 5). This scenario also supports a recent change in the TMVB effective population size during the Wisconsin Glacial stage at 40 kyr (95% CI: 3500 yr – 122 kyr; Additional files 4 & 5).

The best scenario for *Eupherusa* including *T. ridgwayi* (Additional file 5: Fig. 10) was scenario 2 (PP = 0.712, 95% CI: 0.7 – 0.72; Figure 4e). Type I and II errors indicate high confidence in scenario choice (Additional file 3). Scenario 2 suggested divergence of *T. ridgwayi* and a hypothetical ancestral population during the late Pliocene at (*t4*) 2.7 Myr (95% CI: 2.1 – 3.4 Myr), in time (*t3*) and before major climatic oscillations in the mid-Pleistocene, the ancestral *Eupherusa* lineage splits into two hypothetical ancestral lineages, one that further splits at *t2* (~1.3 Myr) giving rise to the populations in eastern Mexico and Central America (*E. eximia–E.nigriventris*), and the second which splits into populations in the SMS (*E. poliocerca-E. cyanophrys*) at 716 kyr (95% CI: 123 kyr – 1.5 Myr; Table 5). When *T. ridgwayi* is excluded (Additional file 5: Fig. 11), the best-supported was scenario 1 (PP = 0.868, 95% CI: 0.859 – 0.877; Figure 4f), which is similar to the previous scenario. Confidence in scenario choice was high given low values of type I and II errors (Additional file 3). Mean parameter estimates of scenario 1 (Table 5) indicated an initial divergence at *t3* (~1.7 Myr) of an ancestral *Eupherusa* lineage into two ancestral populations. One diverged into eastern Mexican and Central American populations at *t2* (~1.2 Myr), whereas the other splits into southwestern Mexican populations at 688 kyr (95% CI: 116 kyr – 1.5 Myr; Additional files 4 & 5).

Test of simultaneous divergence

The hABC analyses including four population pairs spanning along two identified putative barriers (Balsas Depression and Oaxaca's Valleys), showed a relatively strong posterior probability support for four independent divergence events ($PP_{\Psi=4}$ = 0.417) and the highest mode model-averaged posterior estimate of the hyperparameter Ω= 0.1415 (95% HDP interval= 0.0035 – 0.2998), in comparison with posterior probability of two ($PP_{\Psi=2}$ = 0.282) or three ($PP_{\Psi=3}$ = 0.275) divergence events (Figure 5a).

Subsequently, we tested subsets of the data set for simultaneous divergence. First we tested two taxon pairs within SMS (Guerrero and Oaxaca populations separated by the Río Verde drainage) of *Aulacorhynchus* and *Chlorospingus*, obtaining high support for a single divergence event ($PP_{\Psi=1}$ = 0.6749), along with a mode value of Ω consistent with synchronous divergence (Ω= 0.000475) and an Ω= 0, which is included within the 95% HDP intervals (Figure 5b), whereas when including the *Eupherusa* taxon pair (*cyanophrys-poliocerca*), we found low support for a single divergence event, suggesting two divergence events across these taxa ($PP_{\Psi=2} = 0.5436$) and a Ω mode of 0.05 consistent with asynchronous divergence (Figure 5c).

When evaluating southwestern SMS against eastern populations spanning Oaxaca's Central Valley barrier, there was a relatively strong support for a single divergence event between these populations ($PP_{\Psi=1} = 0.4536$) and $\Omega = 0.0022$, also indicating support for synchronous diversification between these taxa occurring at ~1.06 Myr (Figure 6d). Finally, the evaluation of population pairs distributed along Central America revealed a very high posterior probability of one divergence event ($PP_{\Psi=1} = 0.7228$), and a Ω hyperparameter value = 0 (95% HDP interval= 0.0 – 0.1167) across the Nicaraguan Depression lowlands between Costa Rica and Nicaragua occurring ~0.924 Myr (Figure 6e).

Discussion

The aim of comparative phylogeography is to detect concordant patterns among co-distributed species, based on the idea that they may share common histories [1,14,16]. Thus, finding similar genetic patterns among different species may suggest similar historical processes influencing major biological components in a given region. Nevertheless, as shown in the results presented herein, complete concordance is commonly non-existent, which is probably a result of intrinsic characteristics of species triggering different responses to particular events, therefore emphasizing the role of idiosyncratic events in the recent evolutionary history of genetic loci and bird taxa in the region [14,55].

Our study also indicates that at least two unrelated bird genera (*Aulacorhynchus* & *Chlorospingus*) with distinct natural histories and which inhabit roughly the same regions in the humid montane forests of Mesoamerica, present highly similar phylogeographic structure, including a significant split between the highlands in Guerrero and Oaxaca within the SMS, which may be expected due to discontinuous distribution ranges, as well as to their presumably reduced dispersal abilities. The pattern observed in *Cardellina* and *Eupherusa* do not fully agree with the expectation that the degree of isolation between montane ranges is responsible for shaping the genetic differentiation between populations, as has been reported in previous studies of montane birds (see [42,121]), analyses in these two taxa evidenced exclusive haplotypes from Oaxaca, but genetic differentiation across the Río Verde drainage, as seen in *Aulacorhynchus* and *Chlorospingus* does not occur. Regarding *Cardellina*, despite the fact that the TMVB and the SMS montane ranges are separated by a significant geographic barrier such as the Balsas Depression (see [7]), incomplete lineage sorting between both regions is reported.

Phylogenetic and population structure analyses

Our results, as several others from the Neotropics (see [11,13,28,122,123]), found shared phylogeographic breaks at which genetic differentiation occurs among widespread Mesoamerican highland bird species. We observed major breaks, as seen in *Aulacorhynchus* and *Chlorospingus*, between Chiapas and Mexican-Central American lineages. This has been also supported by other bird species [121], plants [28], rodents [18,34], insects [48] and a snake [124]. Moreover, phylogeography shows isolation between populations inhabiting the mountains of south-western Mexico (SMS) and northern Oaxaca (see *Chlorospingus*) evidencing that populations are clearly sorted within Oaxaca across its Central Valley, and more importantly morphological variation of these populations has also been documented as in *E. eximia nelsoni* [125]. Isolation between Central American highland populations (NCA-SCA) has been likely promoted by the Nicaraguan Depression (see [13,123,126]). The most relevant break in our study, occurred within the SMS region, between the states of Oaxaca and Guerrero highlands, which are separated by the Río Verde drainage, this break is supported by studies in plants [32], lizards [127,128], frogs [30] and even in lowland species, such as iguanas [129].

The patterns observed in the haplotype networks mostly reveal a consistent match between haplogroups and subspecies, as well as species boundaries (see *Eupherusa*). The overall structures in the haplotype networks resemble an expected pattern for ancient divergence among the sky-islands where reciprocally monophyletic groups occur on each sky-island with no mixing (see *Aulacorhynchus* and *Chlorospingus*), and is consistent with estimated divergence and the gradual cooling occurring in the Gelasian stage of late Pliocene-early Pleistocene [130]; whereas in *Eupherusa* it is difficult to discern specific events for each divergence estimate due to wide confidence intervals. *Cardellina* is an exception which resembles a star-shaped network of a post glacial sky-island divergence [50] which is consistent with an interglacial period during the Pre-Illinoian stage [130,131] and the estimated divergence in BEAST and DIYABC analyses.

AMOVA results highlighted the existence of genetic structure for all studied species. Most molecular variation was found among groups; nevertheless, the fixation indices (F_{SC}) among populations within groups were significant, as in *Aulacorhynchus*, *Chlorospingus* and *Cardellina*. This pattern suggests the existence of further structured populations in at least one of the defined clusters, as supported by haplotype networks (Figures 2d, 3d).

We obtained overall high values of haplotype diversity (Hd) and low nucleotide diversity (π) for the majority of analyzed groups within each taxon. These patterns have been attributed to population growth following demographic bottlenecks enhancing retention of novel mutations [132,133], which is congruent in sky-island populations supporting lower nucleotide variation given reduced gene flow to other populations [49,134,135]. Population expansions may have been promoted by climatic oscillations during the Pleistocene; nevertheless, we found significant support for population expansion only in *Cardellina* populations from the TMVB, and SMS. For the rest of the taxa, Tajima's D and Fu's F_S values suggest that the observed nucleotide polymorphism is selectively neutral even when they tend towards negative figures, thus favoring demographic stability during the Pleistocene. Pairwise comparisons of F_{ST} values for each taxon are high and mostly significant, which is expected given their disjunct geographic distribution. Overall, all populations concerned are allopatric and several lineages possess phenotypic and phylogenetic identity, thus the F_{ST} fixation indices support the idea that these populations have followed their own evolutionary trajectory for a long time (Tables 3, 4). Despite the F_{ST} pairwise comparison between SMS and TMVB populations was low; according to [91] these populations have great genetic differentiation. Moreover, some populations, despite allopatry, may be geographically close enough to show evidence of intermittent connections in response to environmental changes [136].

Divergence time estimation and Coalescent-based estimation of population history

Our results highlight the importance of Pliocene-Pleistocene events in promoting the intra-specific genetic structure in the analyzed species, as reported in other studies. Divergence between SCA and northern populations is concordant with the formation of the Nicaragua Depression (ca. 4 Myr; [137]), furthermore, divergence between NCA and Mexican lineages post-date the time frame of the formation of the volcanic arcs in Central America (Miocene-Pliocene or before; [137]), the IT dry plains (ca. 6-3 Myr; [36]), orogeny of SMS (ca. 35-20 Myr), and the formation of the TMVB as well as its period of volcanism in central Mexico (ca. 16-7 Myr; [37-39,138,139]). Our results suggest that these geographic breaks may have acted indirectly as semi-permeable barriers to dispersal, leading to an accumulation of processes involving isolation and expansion [140], as the *Cardellina* analyses revealed.

DIYABC scenarios allowed us to infer evolutionary processes affecting populations. Although estimated divergence dates varied among populations of the analyzed taxa, major splits occurred during the Pleistocene. Scenarios from *Aulacorhynchus*, *Chlorospingus*, and *Cardellina,* along with their respective pairwise F_{ST} comparisons, support the hypothesis of sequential northward population range expansions from Central America with ancestral populations being split by vicariant events, such as fracture and changes in altitudinal ranges of montane forests linked to climatic oscillations, therefore promoting geographical isolation. Although our analyses support a southern origin, the pattern observed in *Eupherusa* + *Thalurania ridgwayi* suggest alternative scenarios as also probable. Based on previous evidence supporting *T. ridgwayi* as a member of the *Eupherusa* genus [71,72], we included samples of *T. ridgwayi* in the diversification scenario comparisons, and we were unable to discern if diversification according to the best-supported scenario occurred from two potential regions that may have served as refugia (one in northwestern Mexico, another in southern Mexico-Central America), or whether SMS (*E. poliocerca-E. cyanoprhys*) and Central American lineages of *Eupherusa* come from a migration event from northwestern Mexico. Further studies should focus on the reconstruction of ancestral areas of distribution to clarify this issue (see [47]).

Overall, dates from the DIYABC analyses suggest more recent diversification times than our BEAST analyses, thus highlighting the effect that distinct assumed mutation rates have an effect of temporal frame estimation [141]; nevertheless, these values overlap their respective 95% HDP confidence intervals. Even in vicariant events, differences in time estimates can also be due to variance in the coalescent process and related to the demography of each species [28,47], however we acknowledge the inconveniences of single locus based analyses and that distinct calibration for divergence time estimation may yield potential errors, thus future surveys incorporating more data should be able to obtain stronger and more accurate estimates of timing and synchrony of divergence.

Test of simultaneous divergence

Even when species ranges overlap across their distributional areas, some divergence time estimation frames are not congruent with each other, therefore, asynchrony in diversification within Mesoamerica could be depicted as a result of Pleistocene climatic oscillations which promoted rapid pulses of diversification and speciation rates across multiple lineages [13,28,142]. Our analyses including four population pairs detected non-simultaneous divergence events within the Pleistocene, pointing to the existence of several temporal frames where diversification and fixation of genetic differences within the same montane ranges occurred among distinct lineages. Our results also highlight a high probability of simultaneous divergence occurrence between two taxa (*Aulacorhynchus* and *Chlorospingus*) in the SMS region across the Río Verde drainage lowland barrier, with a mean divergence date of 0.9339 Myr, which 95% HDP confidence intervals falls within the estimated divergence dates between the same populations. When *Eupherusa* population pair (*cyanophrys-poliocerca*) was added, estimations supported two diversification events, thus implying that even when the three taxa share their overall distributional ranges in the SMS, they do not fully share a community-wide historical pattern across the landscape.

Even when we do not fully out rule any orogenic effect over the analyzed species, major changes to population structure should be promoted by the onset of climatic oscillations in the Pleistocene, which have been invoked to explain patterns of genetic differentiation in the increasing rates of speciation and diversification in Neotropical biota, given the evidence of a downward altitudinal migration of the forest line which resulted in a montane forest-like dominated landscape in the lowlands with further retreat when temperature raised [143-145]. Although for the *C. rubra* lineage the observed strong signature of expansion in TMVB and SMS populations due to Pleistocene conditions and forest migrations resulted in the admixture of two isolated lineages; our results reveal that demographic dynamics for other species persisted in isolated regions throughout the Pleistocene allowing the evolution of high endemism, which could be an overall result of high effective population sizes.

Genetic endemism as a result of isolation of intraspecific lineages, as seen within the SMS should be considered in conservation measures given that they preserve historical components and maintain the species capability of adaptation [3,63].

Conclusions

Our survey provides a framework for understanding the complex geographic history of Mesoamerica and its role in promoting lineage diversification in birds. From our analyses we recover multiple independently evolving lineages restricted to montane areas across the region, our results also highlight that congruence may be difficult to occur given idiosyncratic life histories of species;

nevertheless, co-distributed taxa will share more common history than a random scenario could predict. Montane regions within Mesoamerica are strong drivers of lineage diversification, and as such our results point into major areas of great genetic diversity and endemism, such as isolated highlands of the SMS in the Mexican states of Oaxaca and Guerrero. Given ancient development of major montane systems, climatic oscillations and orogeny derived conditions were key drivers of diversification between these lineages as splits were calculated to occur mainly within the Pleistocene.

Methods

Sampling and sequence data

We selected four resident and co-distributed avian taxa from the montane forests of Mesoamerica, all of which represent different orders and families (Apodiformes: Trochilidae; Piciformes: Ramphastidae; and Passeriformes: Parulidae and Passerellidae), as well as life histories. Selected taxa include Toucanets (genus *Aulacorhynchus*), the Red and Red-faced Warbler (genus *Cardellina*), Bush-tanagers (genus *Chlorospingus*), and hummingbirds (genus *Eupherusa-Thalurania*). These taxa include at least one differentiated population restricted to the SMS for which we have previous genetic and morphometric information [5,26,65-76]. These studies have also estimated similar Pliocene-Pleistocene divergence times for all of the analyzed taxa.

Phylogenetic and population structure analyses

For each taxon, we retrieved mitochondrial DNA (mtDNA) sequences deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/), and conducted analyses using alignments of concatenated mtDNA loci (Additional file 1). We estimated nucleotide substitution models and partition schemes for each species in PARTITIONFINDER [77], using the Bayesian Information Criterion (BIC) for model selection. Given the10 bp frameshift overlap in the ATPase 8 and 6 genes and the tRNA-Lys gene, we analyzed these as a single genetic region [78,79]. Resultant partition schemes and model substitution parameters were used for conducting a phylogenetic reconstruction using the Bayesian inference approach (BI) for each species, as implemented in MRBAYES 3.2 [80]. We ran two independent searches using four Markov-Chains MonteCarlo for 10^7 generations sampling every 1000 generations. Convergence across runs was evaluated using two methods: a) the examination of the standard deviation of split frequencies (with acceptance values <0.01); and b) by verification of parameter estimates in TRACER v1.6 [81], based on acceptable effective sample sizes (ESS values > 200). After checking for convergence, the first 25% of the generated trees were discarded as burn-in and the remaining 75% were kept to calculate posterior probabilities. In addition, we also estimated phylogenetic trees using maximum likelihood (ML) criteria, as implemented in RAXMLGUI 1.5b1 [82-84], using the GTRCAT model, and estimated nodal support via 1000 bootstrap iterations using the selected partition. We selected closely-related taxa as outgroups, as suggested by previous published studies: *Aulacorhynchus albivitta* [74], *Chlorospingus flavopectus phaeocephalus* [66], *Cardellina versicolor* [5], and *Thalurania ridgwayi* [71,72].

We used NETWORK 4.6.1.1 (Fluxus Engineering, www.fluxus-engineering.com) to visualize the relationships among haplotypes by constructing networks using the median-joining algorithm [85,86], assigning equal weights to all variable sites and an epsilon parameter with default values (ε=0).

To explicitly test for phylogeographic structure in each taxon avoiding a priori criteria to delineate populations, we used a Bayesian model-based clustering algorithm, as implemented in GENELAND 4.0.3 [87,88], which assigns samples to clusters (K) according to both geographical adjacency and genetic similarity through simulations with the Reversible Jump Markov Chain MonteCarlo (RJMCMC) algorithm. We varied the maximum number of expected clusters (K_{max}) from 2 to 10, following possible sub structuring of populations within the main montane ranges in Mesoamerica. We performed 10 independent runs of 10,000 iterations each, a thinning value of 1000 and a 10% burn-in. Best results were selected according to highest posterior probabilities.

Genetic structure was assessed through hierarchical analysis of molecular variance (AMOVA) using pairwise differences, based on the number of clusters (K) obtained by GENELAND for each taxon. Following these results, samples of *Aulacorhynchus* were divided into four population groups (K=4): 1) Sierra Madre del Sur (SMS) samples from the Mexican states Guerrero and Oaxaca, 2) eastern Mexico and north Central America (EMx-NCA), 3) Costa Rica and northern Panama (CR-NP), and 4) southern Panama (SP); for *Chlorospingus*, we obtained K=6: 1) SMS (Guerrero-Oaxaca), 2) northern Chiapas (including the Chimalapas region in Oaxaca), 3) northeastern Oaxaca and Sierra Madre Oriental (SMO), 4) Los Tuxtlas Massif (TM), 5) northern Central America (NCA), and 6) southern Central America (SCA). Samples of *Cardellina* were divided into K=4: 1) Trans Mexican Volcanic Belt (TMVB), 2) SMS, 3) Sierra Madre Occidental (SMOc), and 4) northern Central America (NCA-*C. versicolor*). Finally, the *Eupherusa-Thalurania* samples, where GENELAND clustering followed current species delimitation: 1) *E. cyanophrys* (Sierra de Miahuatlán, Oaxaca), 2) *E. poliocerca* (Guerrero-Oaxaca), 3) *E. eximia* (N Oaxaca-N Central America), 4) *E. nigriventris* (Costa Rica-Panama), and 5) *Thalurania rigdwayi* (Jalisco).

We also assessed genetic diversity of each population group within each species through the estimation of haplotype diversity (Hd), and nucleotide diversity (π). Genetic divergence between groups was measured using pairwise F_{ST} fixation index [89,90], interpreting the results following guides in [91]. Significance of F_{ST} tests was assessed using 1000 permutations. To test for evidence of recent demographic changes in the selected species, we estimated historical demographic dynamics through the calculation of Fu's F_S statistic [92] and Tajima's D statistic [93] neutrality tests. Significance of these tests ($p<0.02$ in the case of F_S statistic) was calculated through 1000 simulations. All analyses were conducted in ARLEQUIN 3.1 [94].

Divergence time estimation

We used a Bayesian MCMC-based approach to calculate divergence times among haplogroups within each species independently using BEAST v1.8.4 [95]. For each selected taxon, we first tested whether our dataset fits either to a strict clock model or to a relaxed clock model. We performed selection tests through the stepping-stone method (SS; [96]), as implemented in MRBAYES 3.2 [80]. Given our partitioning models, the mean marginal likelihood of a strict clock performed better than a relaxed clock model for all taxa (Additional file 2). Thus, chains were run using a UPGMA starting tree, under a strict clock with substitution models (according to results from PARTITIONFINDER) for 10^8 generations sampling every 1000 steps, using a Yule speciation process [97,98] with no topological constraints, and discarded the first 25% as burn-in. We used two approximations to convert branch lengths into time: (A) a body mass-corrected molecular clock rate of 0.0042 (min=0.0011, max=0.0158) subs/site/Myr [99], and (B) an uncorrelated lognormal relaxed clock substitution rate fixed at 0.01 average subs/site and SD=0.003 [100-102] for each locus calculated in BEAST v1.8.4 [95]. Adjustment of the body mass-corrected and calculated clocks was evaluated using Bayes factors (BF), calculated from the marginal likelihoods from path sampling (PS) and stepping-stone (SS) methods in BEAST v1.8.4 [95,103,104]. Each marginal likelihood was estimated through 100 path steps with a Beta distribution (0.3, 1.0). We considered a 3 Log ml difference as strong evidence [105] against the null hypothesis (Additional file 2). We checked for stationarity using TRACER v1.6 [81]. Node ages are presented as mean heights and 95% credibility interval values with a posterior probability limit of 0.5 and resumed in a maximum clade credibility tree (MCCT). All of these were generated using TREEANNOTATOR v1.8.4 [95], and trees were visualized in FIGTREE v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

Coalescent-based estimation of population history

We tested for different hypotheses of population divergence and admixture using an approximate Bayesian computation (ABC) approach in DIYABC 2.1.0 [106]. We conducted initial simulations using 15 competing evolutionary scenarios per species (Additional file 3). Evolutionary scenarios for each species were built considering results of the phylogenetic and GENELAND analyses, biogeographic diversification scenarios proposed in previous studies (see [68,70,76]), and geographical breaks invoked as responsible of diversification events. We followed recommendations in [47,107,108] for the assessment of appropriate priors, as well as to select the highly-informative summary statistics from the simulations resembling datasets similar to the empirical ones. When phylogenies suggested the existence of two genetic groups within the SMS (p. e. distinctive Guerrero and Oaxaca lineages, as in *Aulacorhynchus* and *Chlorospingus*), we contrasted the same scenarios considering those clades as different populations in the analyses. All competing scenarios were eliminated in successive rounds, where the preferred hypotheses were the ones with highest posterior probabilities.

From the selection process described above, we tested three final models for *Aulacorhynchus*, *Chlorospingus*, and *Cardellina*; and two for *Eupherusa-Thalurania* (Additional file 5). For each matrix analyzed, we simulated 1×10^6 datasets and obtained summary statistics per scenario in each simulation. Based on rates reported previously for birds [109-113], we used an HKY mutation model with a uniform prior distribution, a mean mutation rate with a gamma distribution set to 2.0×10^{-8} substitutions/site/year (min= 1.6×10^{-8}, max= 2.9×10^{-8} substitutions/site/year) The posterior probabilities of competing scenarios were computed using a logistic regression on the 1% of simulated datasets closest to the observed data. The selected scenario was that with highest probability value and a non-overlapping 95% confidence interval. For the best supported scenario, we performed a model-checking procedure using a Principal Components Analysis (PCA) on test statistics to visualize the fit between simulated and observed datasets. Confidence on the chosen scenario was assessed though the calculation of type I and type II error rate, from 500 simulated pseudo-observed datasets (PODs) generated with the data of the best-supported scenario [114,115]. Point estimates for demographic and temporal parameters were obtained by local linear regression on the 1% of simulations closest to the observed dataset for the best-supported scenario [106]. Divergence time obtained from DIYABC output was transformed assuming a conservative two-year generation time, which has been previously used in similar species groups [63,116].

Test of simultaneous divergence

We tested whether genetic differentiation occurred simultaneously between the main geographical barriers in the analyzed clusters by performing a hierarchical approximate Bayesian computation (hABC) analysis as implemented in MSBAYES [4]. Populations inhabiting the montane regions throughout the study area showed similar patterns of genetic structuring even when they are not closely related, we may therefore expect inter-specific simultaneous divergence among regions if the processes driving diversification are common. We performed hABC analyses in 15 population pairs that spanned the same putative barriers to gene flow: between populations within the SMS in south-western Mexico; between populations of the SMS and eastern populations across a lowland barrier in Oaxaca’s Central Valleys, and between populations spanning the Nicaraguan Depression in Central America (Figure 1).

We used jModelTest [117,118] to estimate a transition-transversion rate for each population pair, as required by MSBAYES. The analyses involved the estimation of a vector of summary statistics from the sequences utilized; afterwards $1\mathrm{x}10^6$ data sets were simulated under the specified multi-taxon model using prior distribution for the demographic parameters. The prior of the maximum possible number of divergence events (Ψ) was set to be equal to the number of lineage pairs tested. For the last stage of the MSBAYES analyses, we used the acceptance/rejection algorithm to approximate the posterior distribution for the hyper parameters that characterize the degree of variability of demographic and temporal parameters given the empirical data (e. g., τ, Ψ, Ω). We used Ω estimates to evaluate the support for each hypothesis: synchronous diversification is expected when $\Omega \leq 0.01$; asynchronous diversification if $\Omega > 0.01$ [4,28,119,120]. To estimate mean divergence times, we converted model-averaged $E(\tau)$ estimates (provided in MSBAYES as coalescent units of $4N_{AVE}$ generations) to absolute time (T_{div}), using the equation $T_{div} = E(\tau)\times(\theta_{AVE}/\mu)\times g$, where g is the generation time in years, and θ_{AVE} is the mean of the upper θ prior [119], and μ is the mutation rate. We used a mean mutation rate of 0.0042 substitutions/site/Myr prior [99], and an average generation time of two years [63,116].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

All of the data generated or analyzed during this study are included in this published article [and its supplementary information files].

Competing interest

The authors declare that they have no competing interests.

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Authors' contributions

AR-M and AGN-S conceived and designed the study. AR-M conducted the analyses with input from LAS-G, CG, and AGN-S. AR-M wrote the manuscript with contributions from all of the authors, who read and approved the final manuscript.

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Authors' information

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FIGURE LEGENDS

Fig. 1. Map of Mesoamerica showing the distribution of montane regions for which genetic data were analyzed in the present study, and summary of the main geographic groups in which they were divided. Highlighted in orange is depicted the SMS region and main geographical breaks are show with red lines. Evaluated barriers in this study are numbered as follows: 1) Balsas Depression, 2) Río Verde

drainage, 3) Oaxaca's Central Valley, 4) Isthmus of Tehuantepec, 5) Nicaragua Depression, and 6) Panama Channel Fault Zone (PCFZ).

Fig. 2. Geographical distribution of sampled haplotypes for (a) *Aulacorhynchus* and (b) *Chlorospingus*. (c) and (d) depict median-joining network of concatenated mtDNA loci for *Aulacorhynchus* and *Chlorospingus*, numbers on lines depict mutational steps between haplotypes, gray dots represent median vectors inferred for the data. (e) and (f) depict maximum clade credibility trees using BEAST with branch support (BI/bootstrap). Values between brackets indicate the 95% highest posterior densities (HDP) of the estimated times of divergence events (in Myr). Nodes that have no represented time frame of diversification are those whose lower and upper bounds of the HDP interval had posterior probabilities inferior to 0.5.

Fig. 3. Geographical distribution of sampled haplotypes for (a) *Cardellina* and (b) *Eupherusa* species. (c) and (d) depict median-joining network of concatenated mtDNA loci for *Cardellina* and *Eupherusa* respectively, numbers on lines depict mutational steps between haplotypes, gray dots represent median vectors inferred for the data. (e) and (f) depict maximum clade credibility trees using BEAST with branch support (BI/bootstrap). Values between brackets indicate the 95% highest posterior densities (HDP) of the estimated times of divergence events (in Myr). Nodes that have no represented time frame of diversification are those whose lower and upper bounds of the HDP interval had posterior probabilities inferior to 0.5.

Fig. 4. Best-supported biogeographic scenarios of diversification in analyzed species. (a) scenario 1 of diversification for *Aulacorhynchus*. (b) Scenario 2 of diversification for *Aulacorhynchus* considering as distinct populations lineages from Oaxaca and Guerrero. (c) Scenario 1 of diversification of *Chlorospingus* species. (d) best-supported scenario in *Chlorospingus* considering lineages of Guerrero and Oaxaca as distinct populations. (e) Scenario 2 of diversification in *Eupherusa* species including *T.*

ridgwayi. (f) Scenario 1 of diversification in *Eupherusa* excluding *T. rigdwayi*. (g) Scenario 3 of diversification in *Cardellina* species.

Fig. 5. Joint posterior probability for $E(\tau)$ (average divergence time) and Ω (variance in divergence times/average divergence time) for (a) Four population pairs spanning across southwestern Mexico and eastern-central Mexico through Central America. (b) Two population pairs within SMS. (c) Three population pairs within SMS.

Fig. 6. Joint posterior probability for $E(\tau)$ (average divergence time) and Ω (variance in divergence times/average divergence time) for (d) Three population pairs spanning across southwestern Mexico and eastern Mexico through Central America. (e) Three population pairs in Central America.

Table 1. Hierarchical AMOVAs for each matrix analyzed showing as sources of variation F_{CT}, F_{SC} and F_{ST} respectively.

Table 2. Summary statistics of each analyzed species populations, based on K groups observed in phylogenetic and Geneland analyses, using concatenated mtDNA. N = number of sequences, Hd = haplotype diversity, π = nucleotide diversity. Fu's $\mathrm{F_S}$ and Tajima's D values with an asterisk (*) represent significant values for their respective confidence intervals (< 0.02 and < 0.05). Columns with "n. a." represent null genetic variation owing to the presence of only one haplotype. Region abbreviations are as follows: TMVB = Trans Mexican Volcanic Belt, SMS = Sierra Madre del Sur, SMOc = Sierra Madre Occidental, SMO = Sierra Madre Oriental, NCA = northern Central America, SCA = southern Central America, EMx-NCA = eastern Mexico-northern Central America, CR-NP = Costa Rica-northern Panama, SP = southern Panama.

Table 3. Pairwise $\mathrm{F_{ST}}$ fixation index used to measure genetic structuring in *Aulacorhynchus* and *Chlorospingus*. Abbreviations correspond to defined geographical groups: EMx-NCA (eastern Mexico-northern Central America), CR-NP (Costa Rica-northern Panama), SP (southern Panama), SMS (Sierra

Madre del Sur), SMO (Sierra Madre Oriental), NCA (northern Central America), SCA (southern Central America). An asterisk (*) represents significant values (<0.05).

Table 4. Pairwise F_{ST} fixation index used to measure genetic structuring in *Cardellina* and *Eupherusa*. Abbreviations correspond to defined geographical groups: SMOc (Sierra Madre Occidental), TMVB (Trans Mexican Volcanic Belt), SMS (Sierra Madre del Sur). An asterisk (*) represents significant values (< 0.05).

Table 5. Mean time posterior parameter estimates for the best supported scenarios of analyzed species. Estimates are based on the 1% of simulated datasets closest to the observed values. Time (*t*) is set in years.

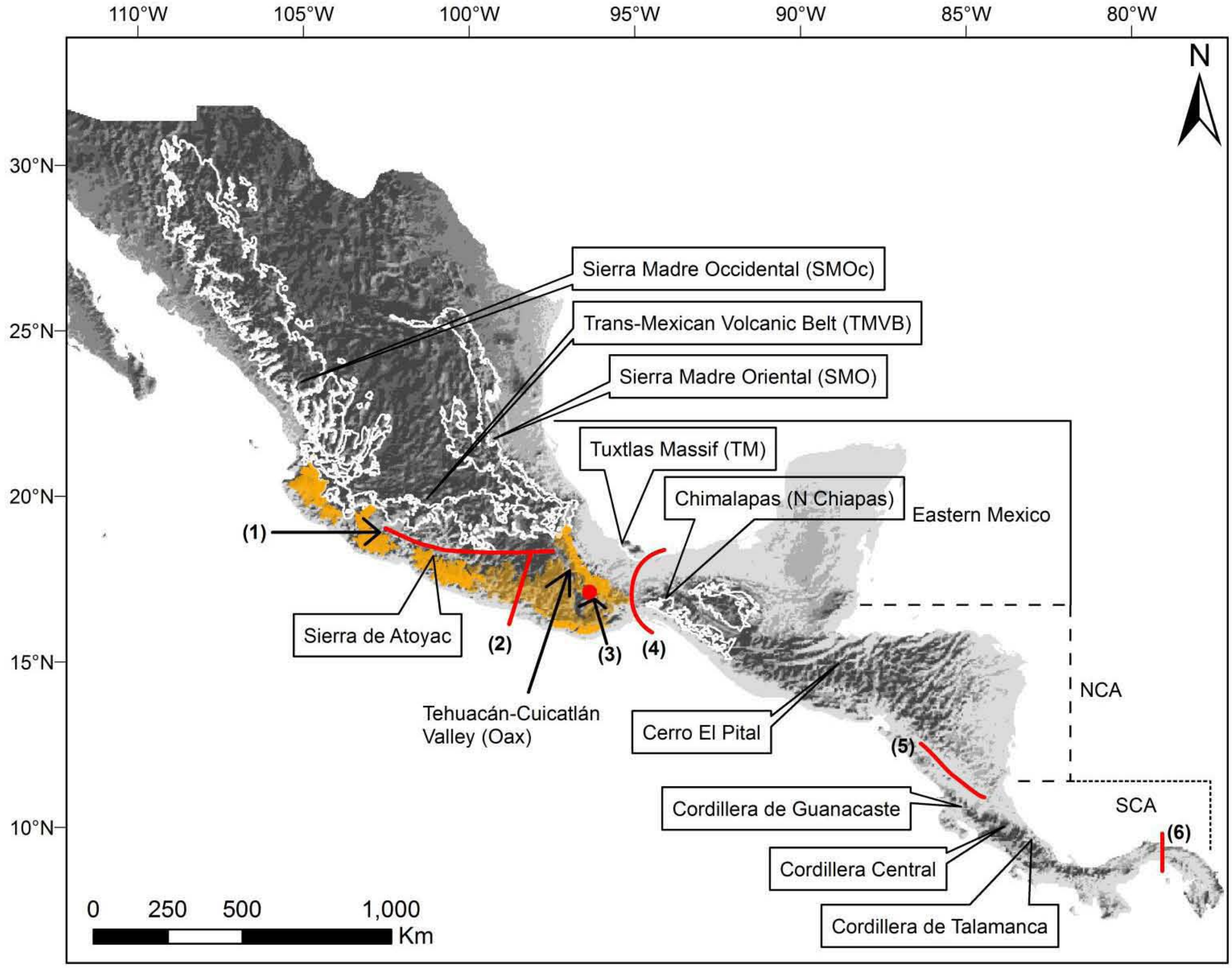
110°W
105°W
100°W
95°W
90°W
85°W
80°W
30°N
25°N
20°N
15°N
10°N
N
Sierra Madre Occidental (SMOc)
Trans-Mexican Volcanic Belt (TMVB)
Sierra Madre Oriental (SMO)
Tuxtlas Massif (TM)
Chimalapas (N Chiapas)
Eastern Mexico
(1)
Sierra de Atoyac
(2)
(3)
(4)
Tehuacán-Cuicatlán Valley (Oax)
Cerro El Pital
NCA
(5)
Cordillera de Guanacaste
SCA
(6)
Cordillera Central
Cordillera de Talamanca
0
250
500
1,000
Km

Fig. 1.

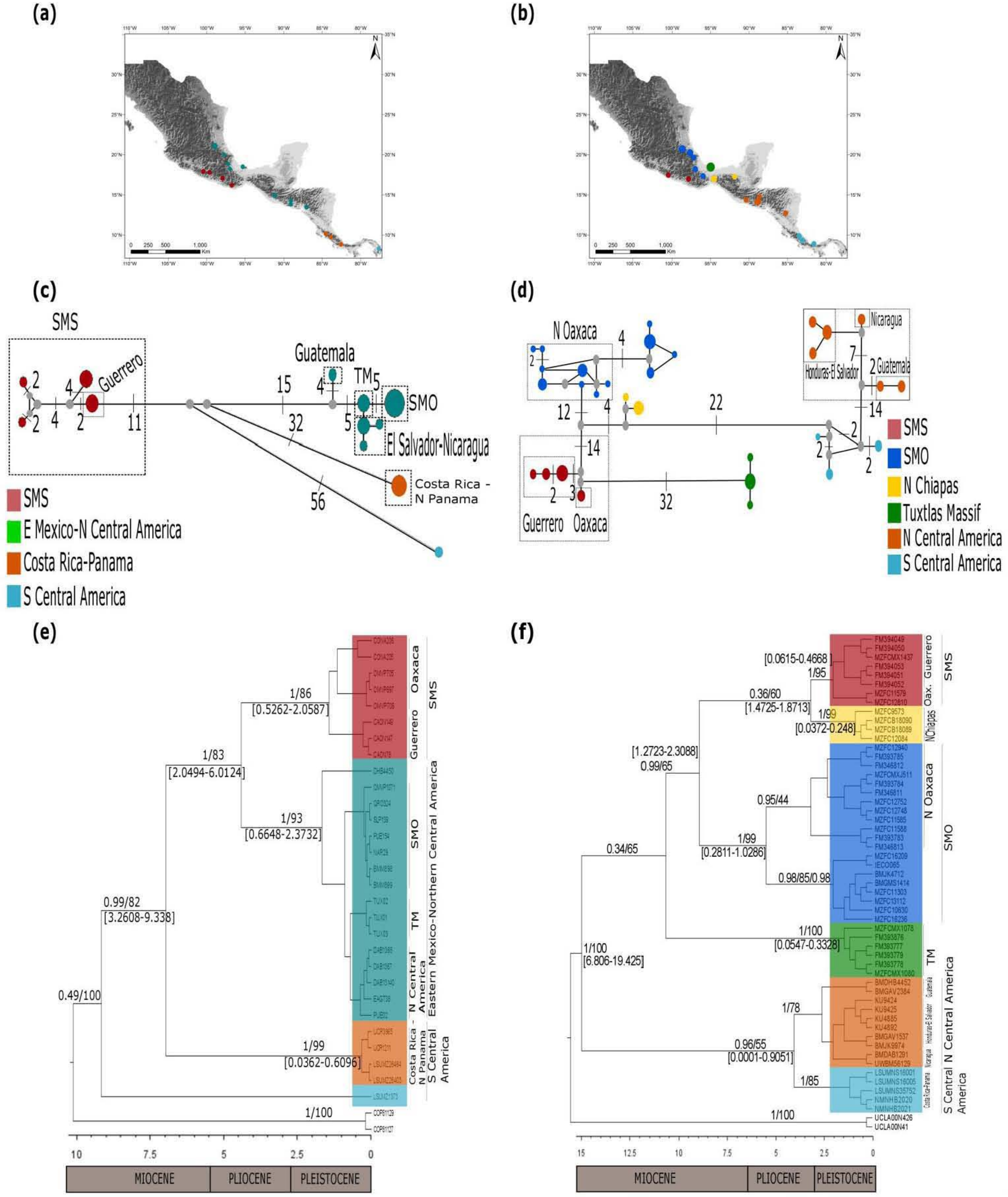
(a)
(b)
(c)
SMS
Guerrero
Guatemala
TM
SMO
El Salvador-Nicaragua
Costa Rica - N Panama
15
32
56
11
SMS
E Mexico-N Central America
Costa Rica-Panama
S Central America
(d)
N Oaxaca
Nicaragua
Honduras-El Salvador
Guatemala
Guerrero
Oaxaca
22
32
14
12
SMS
SMO
N Chiapas
Tuxtlas Massif
N Central America
S Central America
(e)
1/86
[0.5262-2.0587]
1/83
[2.0494-6.0124]
1/93
[0.6648-2.3732]
0.99/82
[3.2608-9.338]
0.49/100
1/99
[0.0362-0.6096]
1/100
Oaxaca
Guerrero
SMS
SMO
TM
N Central America
Eastern Mexico-Northern Central America
Costa Rica - N Panama
S Central America
10
7.5
5
2.5
0
MIOCENE
PLIOCENE
PLEISTOCENE
(f)
[0.0615-0.4668]
1/95
0.36/60
[1.4725-1.8713]
1/99
[0.0372-0.248]
[1.2723-2.3088]
0.99/65
0.95/44
1/99
[0.2811-1.0286]
0.98/85/0.98
0.34/65
1/100
[0.0547-0.3328]
1/100
[6.806-19.425]
1/78
0.96/55
[0.0001-0.9051]
1/85
1/100
Guerrero
Oax.
SMS
NChiapas
N Oaxaca
SMO
TM
Guatemala
Honduras-El Salvador
Nicaragua
Costa Rica-Panama
N Central America
S Central America
15
12.5
10
7.5
5
2.5
0
MIOCENE
PLIOCENE
PLEISTOCENE

Fig. 2.

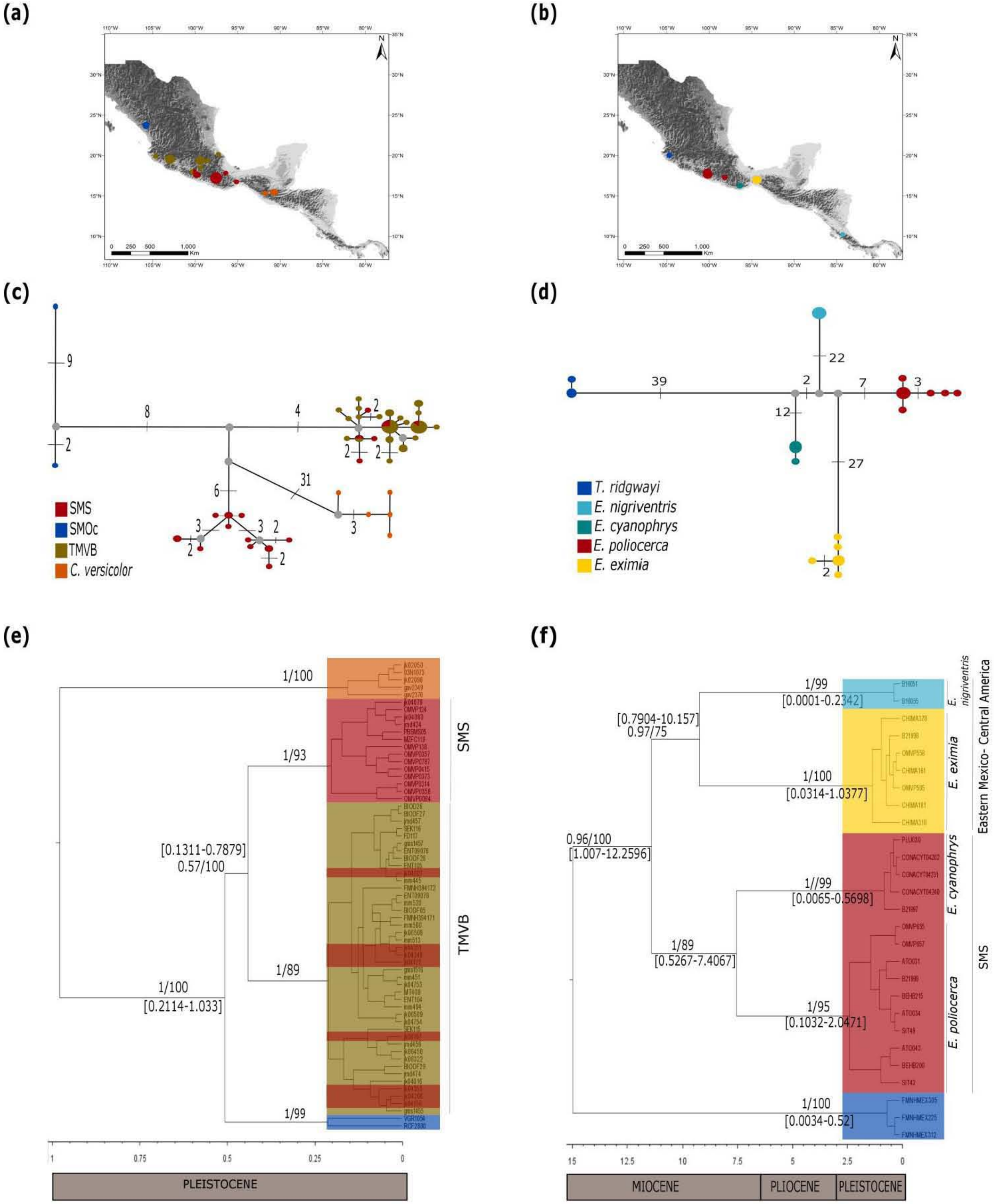
(a)
(b)
(c)
9
8
4
2
2
2
2
31
6
3
3
2
3
2
2
SMS
SMOc
TMVB
C. versicolor
(d)
22
39
2
7
3
12
27
2
T. ridgwayi
E. nigriventris
E. cyanophrys
E. poliocerca
E. eximia
(e)
1/100
1/93
SMS
[0.1311-0.7879]
0.57/100
TMVB
1/89
1/100
[0.2114-1.033]
1/99
1
0.75
0.5
0.25
0
PLEISTOCENE
(f)
1/99
[0.0001-0.2342]
E. nigriventris
[0.7904-10.157]
0.97/75
1/100
[0.0314-1.0377]
E. eximia
Eastern Mexico- Central America
0.96/100
[1.007-12.2596]
1//99
[0.0065-0.5698]
E. cyanophrys
1/89
[0.5267-7.4067]
SMS
1/95
[0.1032-2.0471]
E. poliocerca
1/100
[0.0034-0.52]
15
12.5
10
7.5
5
2.5
0
MIOCENE
PLIOCENE
PLEISTOCENE

Fig. 3.

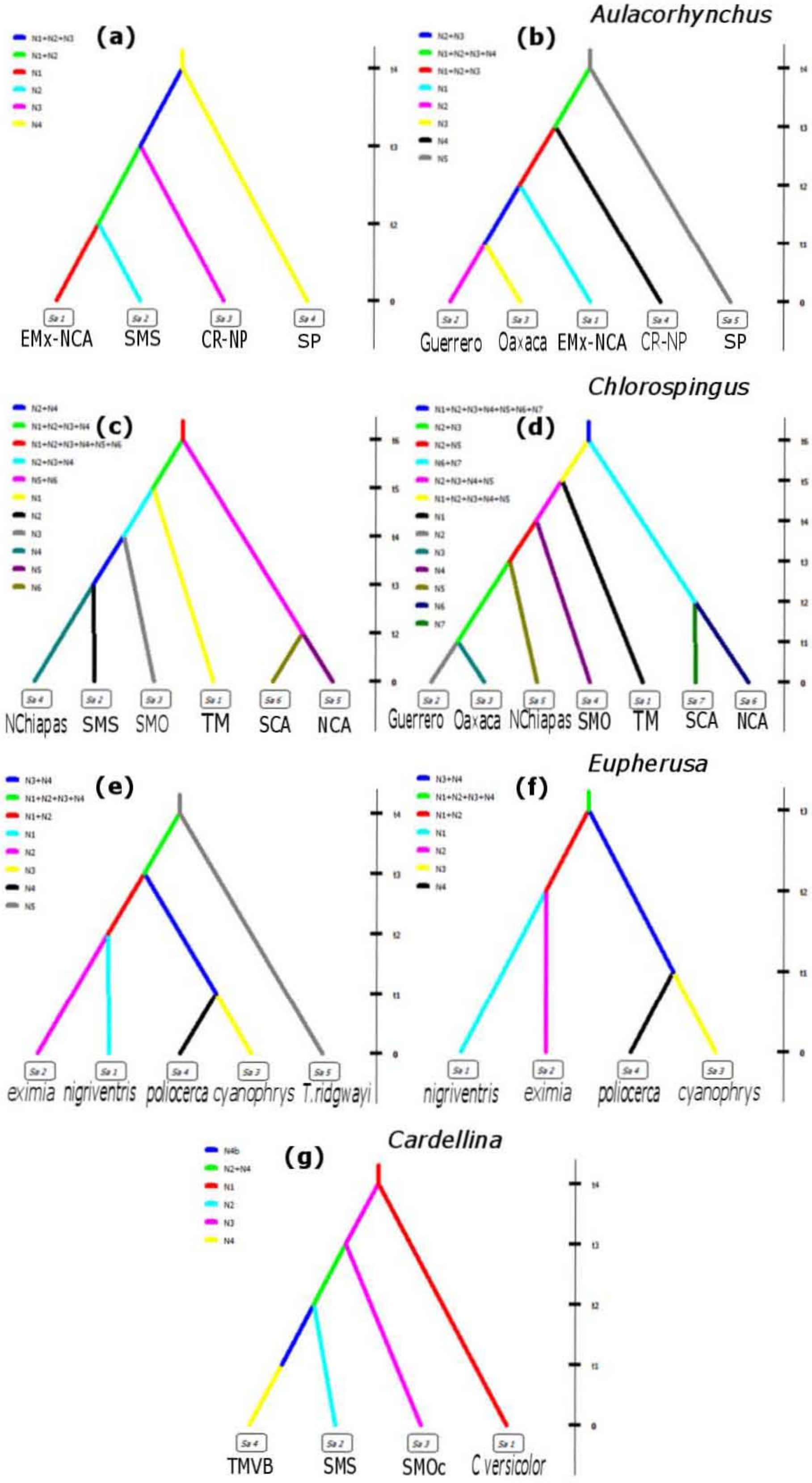
Aulacorhynchus
(a)
N1+N2+N3
N1+N2
N1
N2
N3
N4
t4
t3
t2
0
Sa 1
EMx-NCA
Sa 2
SMS
Sa 3
CR-NP
Sa 4
SP
(b)
N2+N3
N1+N2+N3+N4
N1+N2+N3
N1
N2
N3
N4
N5
t4
t3
t2
t1
0
Sa 2
Guerrero
Sa 3
Oaxaca
Sa 1
EMx-NCA
Sa 4
CR-NP
Sa 5
SP
Chlorospingus
(c)
N2+N4
N1+N2+N3+N4
N1+N2+N3+N4+N5+N6
N2+N3+N4
N5+N6
N1
N2
N3
N4
N5
N6
t6
t5
t4
t3
t2
0
Sa 4
NChiapas
Sa 2
SMS
Sa 3
SMO
Sa 1
TM
Sa 6
SCA
Sa 5
NCA
(d)
N1+N2+N3+N4+N5+N6+N7
N2+N3
N2+N5
N6+N7
N2+N3+N4+N5
N1+N2+N3+N4+N5
N1
N2
N3
N4
N5
N6
N7
t6
t5
t4
t3
t2
t1
0
Sa 2
Guerrero
Sa 3
Oaxaca
Sa 5
NChiapas
Sa 4
SMO
Sa 1
TM
Sa 7
SCA
Sa 6
NCA
Eupherusa
(e)
N3+N4
N1+N2+N3+N4
N1+N2
N1
N2
N3
N4
N5
t4
t3
t2
t1
0
Sa 2
eximia
Sa 1
nigriventris
Sa 4
poliocerca
Sa 3
cyanophrys
Sa 5
T.ridgwayi
(f)
N3+N4
N1+N2+N3+N4
N1+N2
N1
N2
N3
N4
t3
t2
t1
0
Sa 1
nigriventris
Sa 2
eximia
Sa 4
poliocerca
Sa 3
cyanophrys
Cardellina
(g)
N4b
N2+N4
N1
N2
N3
N4
t4
t3
t2
t1
0
Sa 4
TMVB
Sa 2
SMS
Sa 3
SMOc
Sa 1
C versicolor

Fig. 4.

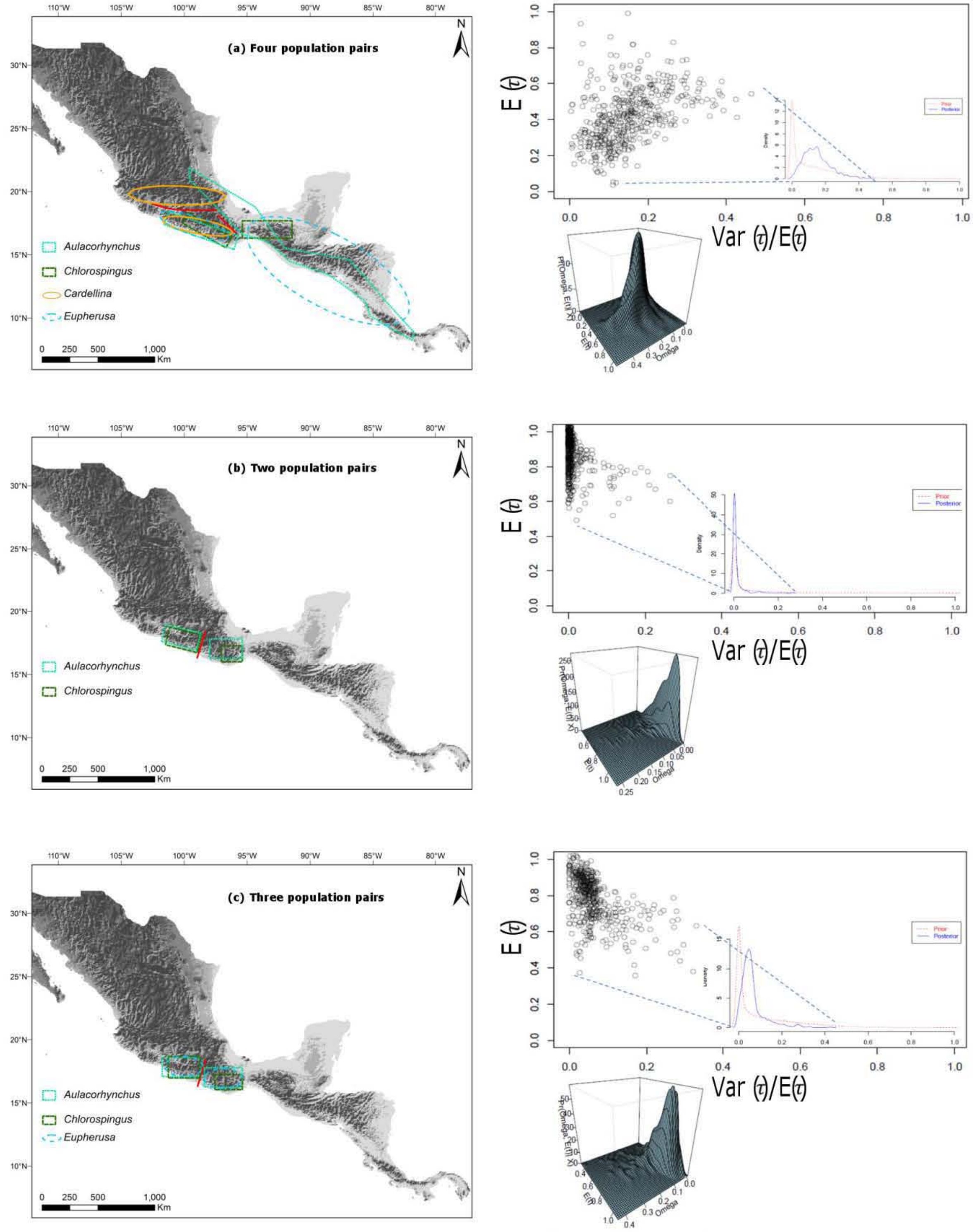
(a) Four population pairs
(b) Two population pairs
(c) Three population pairs
Aulacorhynchus
Chlorospingus
Cardellina
Eupherusa
110°W
105°W
100°W
95°W
90°W
85°W
80°W
30°N
25°N
20°N
15°N
10°N
N
0 250 500 1,000 Km
E (τ)
Var (τ)/E(τ)
Prior
Posterior
Density
Pr(Omega, E(t)|X)
E(t)
Omega

Fig. 5.

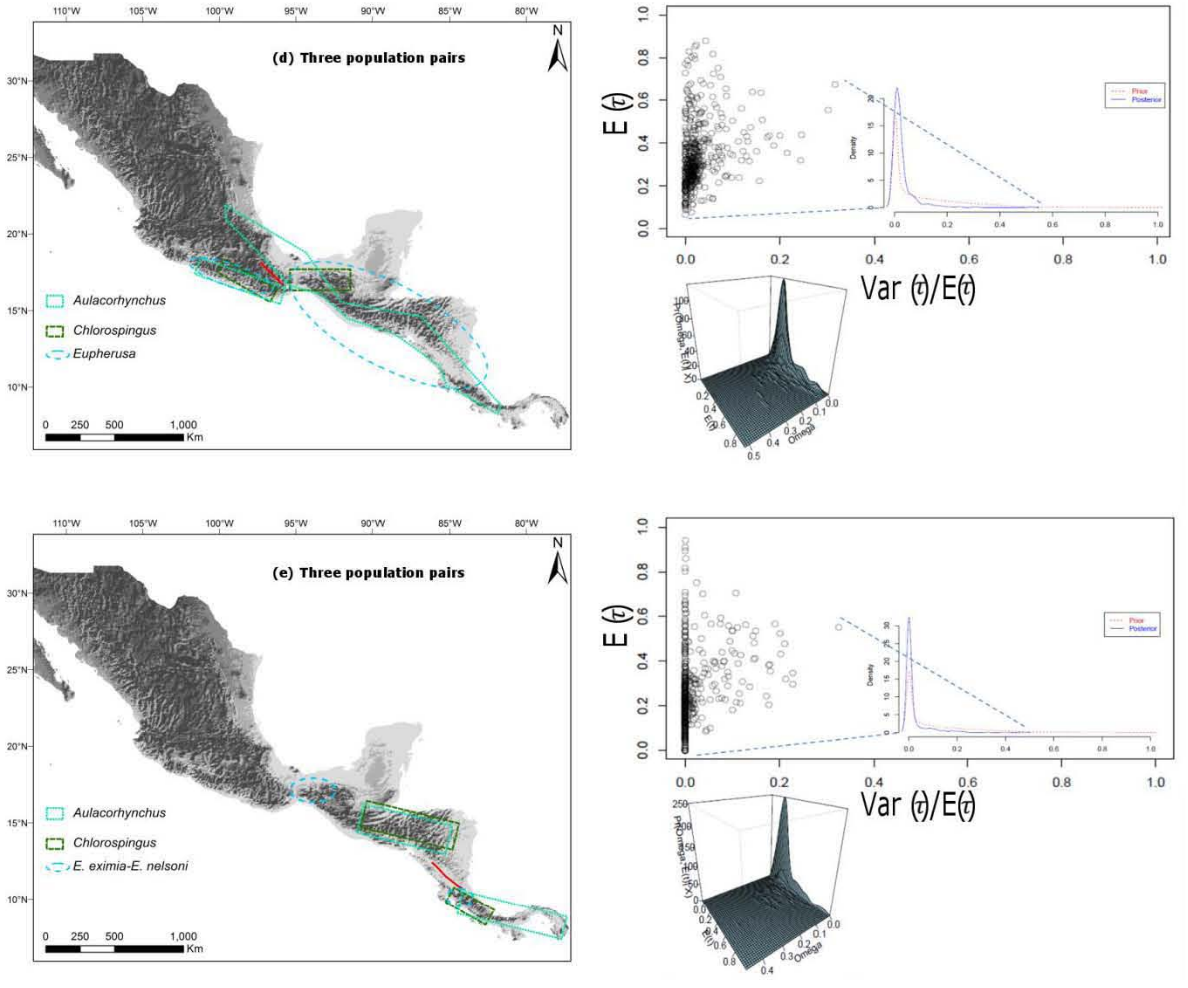
(d) Three population pairs
110°W
105°W
100°W
95°W
90°W
85°W
80°W
30°N
25°N
20°N
15°N
10°N
N
Aulacorhynchus
Chlorospingus
Eupherusa
0 250 500 1,000 Km
E (τ)
Var (τ)/E(τ)
Density
Prior
Posterior
Pr(Omega, E(τ)|X)
E(τ)
Omega
(e) Three population pairs
Aulacorhynchus
Chlorospingus
E. eximia-E. nelsoni
0 250 500 1,000 Km
E (τ)
Var (τ)/E(τ)
Density
Prior
Posterior
Pr(Omega, E(τ)|X)
E(τ)
Omega

Fig. 6.

Dataset	Groupings	Source of variation	Sum of squares	Variance components	Percentage of variation	Statistics	Significance (p)
Aulacorhynchus	(NP) (CR-NP) (EMx-NCA) (SMS)	Among groups	368.978	19.644	84.62	F_{CT}=0.846	0.091
		Among populations within groups	8.928	1.382	5.96	F_{SC}=0.387	<0.00001
		Within populations	52.51	2.187	9.42	F_{ST}=0.905	<0.00001
Chlorospingus	(TM) (N Chiapas) (SMO) (SMS) (NCA) (SCA)	Among groups	702.506	15.108	79.51	F_{CT}=0.795	0.053
		Among populations within groups	7.792	1.949	10.26	F_{SC}=0.5	0.041
		Within populations	89.4	1.943	10.23	F_{ST}=0.897	<0.00001
Cardellina	(TMVB) (SMS) (SMOc) (*C. versicolor*)	Among groups	195.29	12.94493	71.09	F_{CT}=0.71094	0.1564
		Among populations within groups	69.803	2.5099	13.78	F_{SC}=0.47687	<0.00001
		Within populations	162.447	2.753	15.12	F_{ST}=0.84879	<0.00001
Eupherusa	(E.	Among groups	392.306	18.846	93.16	F_{CT}=0.931	0.077

	nigriventris) (E. *cyanophrys*) (E. *poliocerca*) (E. *eximia*) (*T. ridgwayi*)					4	
		Among populations within groups	4	0.654	3.23	F_{SC}=0.472	0.1886
		Within populations	15.324	0.729	3.61	F_{ST}=0.963	<0.00001

Table 1.

Species												
Chlorospingus				***Aulacorhynchus***				***Eupherusa***				
Tuxtlas Massif	N Chiapas	NCA	SCA	SMS	EMx-NCA	CR-NP	SP	*T. ridgwayi*	*eximia*	*poliocerca*	*cyanophrys*	*nigriventris*
6	4	10	5	8	11	4	1	3	7	10	5	2
0.6 (0.215)	0.5 (0.265)	0.844 (0.1029)	0.8 (0.164)	0.785 (0.112)	0.5636 (0.134)	n. a.	n. a.	0.66 (0.314)	0.857 (0.137)	0.77 (0.137)	0.4 (0.237)	n. a.
0.00104 (0.00105)	0.00234 (0.002)	0.0084 (0.005)	0.0095 (0.0062)	0.0055 (0.0033)	0.0045 (0.0026)	n. a.	n. a.	0.0006 (0.0007)	0.0015 (0.00119)	0.0024 (0.0016)	0.0004 (0.0005)	n. a.
-1.131	-0.75445	-0.20935	0.9544	0.734	-0.33	n. a.	n. a.	n. a.	-1.023	0.138	-0.816	n. a.
-0.858	1.716	0.57	3.1833	2.75	5.29	n. a.	n. a.	0.2	-2.019	-1.206	0.09	n. a.

Table 2.

Diversity Indexes						
	Cardellina					
Groups	*C. versicolor*	TMVB	SMS	SMOc	SMO	SMS
N	5	42	14	2	20	8
Hd (S. D.)	1 (0.1265)	0.982 (0.046)	0.967 (0.036)	1 (0.5)	0.931 (0.034)	0.821 (0.1007)
π (S. D.)	0.00126 (0.00092)	0.00264 (0.0015)	0.0021 (0.0012)	0.0046 (0.0048)	0.0083 (0.0047)	0.00518 (0.0033)
Tajima's D	-0.74682	-1.732*	-0.686	n. a.	0.5083	1.0958
Fu's F_S	-2.2375*	-17.67*	-3.874*	2.397	-2.84	1.226

	EMx-NCA	**CR-NP**	**SP**	**SMS**	**SMO**	**Tuxtlas Massif**	**N Chiapas**	**NCA**	**SCA**
Aulacorhynchus									
EMx-NCA	-	0.923*	0.922	0.849*					
CR-NP		-	1	0.907*					
SP			-	0.904					
SMS				-					
Chlorospingus									
SMS				-					
SMO				0.863*	-				
Tuxtlas Massif				0.941*	0.912*	-			
N Chiapas				0.905*	0.839*	0.976*	-		
NCA				0.894*	0.877*	0.911*	0.882*	-	
SCA				0.885*	0.886*	0.928*	0.893*	0.784*	-

Table 3.

	C. versicolor	**SMOc**	**TMVB**	**SMS**	***T. ridgwayi***	***E. nigriventris***	***E. eximia***	***E. poliocerca***	***E. cyanoprhys***
Cardellina									
C. versicolor	-								
SMOc	0.9003*	-							
TMVB	0.93116*	0.82625*	-						
SMS	0.80247*	0.5419*	0.47295*	-					
Eupherusa									
T. ridgwayi					-				
E. nigriventris					0.991	-			
E. eximia					0.975*	0.959*	-		
E. poliocerca					0.952*	0.926*	0.941*	-	
E. cyanophrys					0.99*	0.991	0.972*	0.917*	-

Table 4.

Dataset	Groupings	*t1*	*t2*	*t3*	*t4*	*t5*	*t6*
Aulacorhynchus	Four population groups		1,328,000	2,860,000	4,340,000		
	Five population groups	204,000	1,884,000	2,300,000	3,300,000		
Chlorospingus	Six population groups		1,308,000	2,060,000	2,840,000	3,900,000	5,860,000
	Seven population groups	656,000	1,014,000	1,218,000	1,598,000	1,946,000	2,040,000
Cardellina		40,200	260,000	426,000	1,304,000		
Eupherusa	Including *T. ridgwayi*	716,000	1,346,000	1,804,000	2,780,000		
	Excluding *T. ridgwayi*	688,000	1,290,000	1,724,000			

Table 5.

DISCUSIÓN Y CONCLUSIONES

El objetivo de los estudios de filogeografía comparada es detectar patrones concordantes entre especies co-distribuidas, basándose en la idea de que deberían compartir historias comunes (Avise, 2000; Linder, 2001; Arbeláez-Cortés, 2012). Por lo tanto, encontrar patrones similares entre distintas especies puede sugerir que procesos históricos similares han influenciado los componentes biológicos de una región en particular. Sin embargo, como se muestra en los resultados de este trabajo, no existe concordancia completa, lo cual, debido probablemente a las características intrínsecas de las especies, lo cual resulta en respuestas distintas a eventos particulares y enfatiza el papel que juegan los eventos idiosincráticos en la historia evolutiva reciente de los *loci* y los taxones de la región (Qu y Lei, 2009; Arbeláez-Cortés, 2012). Sin embargo, los resultados, así como muchos otros de los Neotrópicos (*e. g.*, Cabanne *et al.*, 2008; Milá *et al.*, 2009; Ortíz-Ramírez *et al.*, 2016), demuestran rompimientos filogeográficos comunes entre aves montanas ampliamente distribuidas en Mesoamérica.

Los rompimientos filogeográficos en los cuales ocurre la diferenciación genética parecen coincidir con patrones biogeográficos previamente descritos en Mesoamérica (*e. g.*, Sánchez-González *et al.*, 2008). El patrón más relevante para la SMS, ocurrió entre las tierras altas de los estados de Oaxaca y Guerrero en México, que se encuentran separados por el valle del Río Verde. Este rompimiento se encuentra soportado por estudios en plantas (González-Villareal, 2003), lagartijas (Flores-Villela y Sánchez, 2003; Nieto-Montes de Oca *et al.*, 2016), ranas (Campbell *et al.*, 2009) y aún por especies de tierras bajas, como iguanas del género *Ctenosaura* (Zarza *et al.*, 2008). También se observan rompimientos, como en *Aulacorhynchus* y *Chlorospingus*, entre Chiapas y Centro América, patrón observado en aves (Vázquez-Miranda *et al.*, 2009; Ortíz-Ramírez *et al.*, 2016; Zamudio-Beltrán y Hernández-Baños, 2018), plantas (Ornelas *et al.*, 2013), roedores (Harris *et al.*, 2000; Ordóñez-Garza *et al.*, 2010), insectos (Duennes *et al.*, 2012) y reptiles (Devitt, 2006). Además, los análisis en este trabajo revelaron aislamiento entre poblaciones en las montañas del suroeste de México (SMS) y el norte de Oaxaca (ver *Chlorospingus*). Como evidencia correlativa, también se ha documentado variación morfológica en poblaciones del colibrí *E. eximia nelsoni* en la región norte de Oaxaca (Hernández-Baños, 1998). El aislamiento entre las poblaciones de Centroamérica (NCA-SCA) probablemente ha sido promovido por la Depresión de Nicaragua (*e. g.*, Sánchez-González *et al.*, 2008).

Los patrones observados en las redes de haplotipos revelan una relación consistente entre los haplogrupos y subespecies, así como con límites de especies (ver *Eupherusa*). Las estructuras generales de las redes de haplotipos revelan un patrón consistente con divergencia profunda entre las distintas islas (*sky-islands*) donde se encuentran complementos monofiléticos de los haplotipos en cada una sin que ocurra mezcla (ver *Aulacorhynchus* y *Chlorospingus*), así mismo la divergencia estimada concuerda con una etapa de enfriamiento durante la etapa del Gelasiano del Plioceno tardío (Gibbard y van Kolfschoten, 2005). En *Eupherusa* se dificulta distinguir específicamente los eventos relacionados con los tiempos de divergencia estimados, debido a los amplios intervalos de confianza obtenidos. *Cardellina* es una excepción al patrón mencionado anteriormente, ya que la red asemeja un patrón de estrella de divergencia post-glacial en las islas (McCormack *et al.,* 2008), consistente con un periodo interglaciar durante la etapa Pre-Illinoiano (Gibbard y van Kolfschoten, 2005; Lüthi *et al.,* 2008) y la divergencia estimada en los análisis de BEAST y DIYABC.

Los resultados de los AMOVA resaltaron la existencia de estructura genética en todas las especies estudiadas. Mayoritariamente la variación molecular se distribuyó entre poblaciones, como en *Aulacorhynchus* y *Cardellina* lo que revela alta diferenciación entre las distintas regiones montanas. Sin embargo, en *Chlorospingus* y *Eupherusa* se observó que un mayor porcentaje de variación se distribuye entre poblaciones dentro de grupos, lo que sugiere la existencia de mayor estructuración dentro de alguno de los grupos definidos para análisis.

Se obtuvieron altos valores de diversidad haplotípica (Hd) y baja diversidad nucleotídica (π) para la mayoría de los grupos analizados. Este tipo de patrón se ha atribuido a crecimientos poblacionales resultados de cuellos de botella demográficos, lo cual promueve la retención de mutaciones nuevas (Watterson, 1984; Grant y Bowen, 1998). Esto es congruente con las poblaciones distribuidas en *sky-islands* ya que se espera que soporten menor diversidad nucleotídica debido a que no hay flujo génico con otras poblaciones (Frankham, 1997; Barber, 1999; Masta, 2000). Las expansiones poblacionales pueden ser promovidas por oscilaciones climáticas durante el Pleistoceno, sin embargo, solo se ha encontrado soporte para expansión poblacional en las poblaciones de *Cardellina* del *TMVB* (*C. rubra rubra*) y SMS (*C. rubra rowleyi*). Para el resto de los taxones analizados, la D de Tajima y los valores de $\mathrm{F_S}$ de Fu sugieren que el polimorfismo nucleotídico observado es neutral, aun cuando tienden hacia figuras negativas lo cual indica estabilidad demográfica durante el Pleistoceno. En las comparaciones pareadas de F_{ST} se obtienen valores altos y mayoritariamente significativos lo cual es congruente con la distribución disyunta de las poblaciones estudiadas. En general, todas las poblaciones son alopátricas y varios de los linajes poseen identidad fenotípica y filogenética, por tanto, los índices de fijación F_{ST} apoyan la idea que estas poblaciones han seguido su propia trayectoria evolutiva por algún tiempo. A pesar de que el valor de F_{ST} pareado en la especie *C. rubra* entre SMS y *TMVB* es el más bajo obtenido, de acuerdo con Hartl y Clarck (1997), estas poblaciones están muy diferenciadas genéticamente. Algunas poblaciones que habitan ecosistemas aislados con características tipo isla, a pesar de la alopatría, pueden encontrarse lo suficientemente cerca en un contexto geográfico, de modo que pueden ocurrir conexiones intermitentes en respuesta a cambios ambientales (Barker *et al.*, 2012).

Nuestros resultados subrayan la importancia de los eventos del Plioceno-Pleistoceno que promovieron la estructura genética intra-específica en las especies analizadas. La diversificación entre las poblaciones de SCA y las poblaciones del norte concuerda con la formación de la Depresión de Nicaragua (*ca*. 4 Ma; Gutiérrez-García y Vázquez-Domínguez, 2013), así mismo, la diversificación de los linajes de NCA y México ocurre posteriormente a los tiempos estimados de formación de los arcos volcánicos en Centroamérica (Mioceno-Plioceno o antes; Gutiérrez-García y Vázquez-Domínguez, 2013), el Istmo de Tehuantepec (*ca*. 6-3 Ma; Barrier *et al.*, 1998), orogenia de la SMS (*ca*. 35-20 Ma), y la formación del *TMVB* así como su periodo de vulcanismo en el centro de México (*ca*. 16-7 Ma; Morán-Zenteno *et al.*, 1999, 2000; Verma y Carrasco-Núñez, 2003; Bryson *et al.*, 2012; Ferrari *et al.*, 2012).

Los escenarios de DIYABC permitieron inferir los procesos evolutivos que influencian a las poblaciones. A pesar de que la divergencia estimada varió entre poblaciones de los taxones analizados, la mayoría de eventos ocurrió durante el Pleistoceno. Los escenarios para *Aulacorhynchus*, *Chlorospingus* y *Cardellina*, así como los valores de F_{ST} pareados soportan la hipótesis de crecimiento poblacional hacia el norte desde Centroamérica con las poblaciones ancestrales siendo separadas por eventos vicariantes, tales como fractura y cambios altitudinales de los bosques montanos ligados a oscilaciones climáticas que pudiesen promover aislamiento geográfico. Sin embargo, el patrón observado en *Euhperusa* + *T. ridgwayi* puede sugerir alternativas como la existencia de refugios en el noroeste de México y América Central o bien los linajes de *Eupherusa* provienen de un evento migratorio del noroeste mexicano.

Aun cuando las áreas distribucionales de los taxones se sobreponen, algunos tiempos de divergencia estimados no son congruentes entre sí, por tanto, la diversificación asincrónica en Mesoamérica puede ser resultado de las oscilaciones climáticas durante el Pleistoceno que promovieron pulsos rápidos de diversificación y especiación entre múltiples linajes (Ornelas *et al.*, 2013; Ortíz-Ramírez *et al.*, 2016). Los análisis de hABC realizados entre pares de poblaciones distribuidas a lo largo de las mismas barreras geográficas putativas detectaron divergencia no simultánea al analizar cuatro pares poblacionales, lo cual señala la existencia de múltiples marcos temporales en los cuales ocurrió diversificación y fijación de las diferencias genéticas. Los resultados al analizar la diversificación entre pares poblacionales distribuidos dentro de la SMS señalan alta probabilidad de un único evento de divergencia para dos taxones (*Aulacorhynchus* y *Chlorospingus*), sin embargo, al agregar el par poblacional de *Eupherusa* (*cyanoprhys-poliocerca*), se estimó una mayor probabilidad de dos eventos de diversificación, por lo que es posible decir que pese a que estos taxones comparten sus áreas distribucionales dentro de la SMS, no comparten un patrón histórico común a en la región.

Este estudio provee de un marco de referencia para entender la compleja historia geográfica de Mesoamérica y el papel que jugó al promover la diversificación de linajes en aves. De los análisis realizados se han obtenido múltiples linajes restringidos a distintas regiones de montaña a lo largo de la región, los resultados subrayan que la congruencia perfecta no ocurre debido a las historias de vida idiosincráticas de cada especie, sin embargo, los taxones co-distribuidos compartirán más historia en común que lo que podría predecir un escenario al azar. Las regiones montanas dentro de Mesoamérica son fuertes impulsores de diversificación de linajes, y como tal, los resultados apuntan a grandes áreas de diversidad genética y endemismo tales como las tierras altas de la SMS, particularmente los estados de Guerrero y Oaxaca. Dado el antiguo desarrollo de los principales sistemas montanos, las oscilaciones climáticas y las condiciones derivadas de la orogenia fueron factores clave de la diversificación entre estos linajes, ya que se calculó que las divisiones ocurren dentro del Pleistoceno.

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