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

"Diversificación de dos especies del género *Sturnira* (Chiroptera: Phyllostomidae) en Mesoamérica"

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS BIOLÓGICAS

PRESENTA:

GIOVANI HERNÁNDEZ CANCHOLA

TUTORA PRINCIPAL DE TESIS: DRA. LIVIA SOCORRO LEÓN PANIAGUA
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INSTITUTO DE ECOLOGÍA, UNAM

MÉXICO, CD. MX. AGOSTO, 2018

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OFICIO FCIE/DAIP/685/2018
ASUNTO: Oficio de Jurado

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

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **21 de mayo de 2018**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **HERNÁNDEZ CANCHOLA GIOVANI** con número de cuenta **304224669** con la tesis titulada: **"Diversificación de dos especies del género *Sturnira* (Chiroptera: Phyllostomidae) en Mesoamérica"**, realizada bajo la dirección del (la) **DRA. LIVIA SOCORRO LEÓN PANIAGUA:**

Presidente:	**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**
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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Ciudad Universitaria, Cd. Mx., a 25 de julio de 2018

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLOGICAS
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RESUMEN

Mesoamérica, la región que abarca las zonas tropicales desde México a Panamá, es considerada un *hotspot* de biodiversidad y un área rica en endemismos. En esta zona se distribuyen ampliamente dos especies del género *Sturnira*, considerado como el más diverso de todos los murciélagos frugívoros neotropicales, pero del que aún existen controversias sobre las relaciones filogenéticas y límites taxonómicos entre sus especies. Recientemente se sugirió que algunas subespecies mesoamericanas podrían ser reconocidas a nivel específico, una de ellas es *S. hondurensis*, un murciélago asociado a bosques montañosos templados, y la otra es *S. parvidens* asociada a selvas tropicales de tierras bajas. Sin embargo, aún no es conocida la historia evolutiva de estas especies. Por lo anterior, el objetivo de este trabajo fue analizar los procesos evolutivos involucrados en la diversificación de este par de murciélagos, ya que representan un excelente modelo de estudio al habitar en una región donde previamente se han identificado múltiples procesos de diversificación en numerosos taxones. Considerando que estos murciélagos se originaron recientemente (*c.* 2.5 Ma), es posible recuperar gran parte de su historia evolutiva por medio de análisis filogeográficos (factores históricos) y de nicho ambiental (factores ecológicos). Para ello se analizaron sus relaciones filogenéticas, los niveles de variación y estructuración genética, la demografía histórica, así como pruebas de similitud de nicho ambiental en un marco integral. Las dos especies mostraron algunas semejanzas en sus procesos evolutivos, ya que aparentemente solo eventos climáticos severos afectaron sus niveles de estructuración y diversidad genética. Esto propició la diferenciación genética y ambiental dentro de cada especie de un linaje ubicado en el oeste de México. En esta zona se observó una demografía histórica más estable, posiblemente por la compleja topografía que permitió la permanencia de poblaciones durante periodos de cambio climático. Cabe destacar que las características geográficas promovieron la diferenciación intraespecífica en la especie montañosa, mientras que en la especie de tierras bajas estos procesos se relacionan con la divergencia de nicho ambiental en áreas sin evidentes barreras geográficas. Los resultados sugieren que a pesar de existir patrones biogeográficos semejantes, los procesos que los originaron suelen ser especie-específicos en los cuales la biología de las especies es determinante en los mecanismos de evolución biológica. Por otra parte, los resultados reconocen como especies a los taxa Mesoamericanos, además de que esclarecen sus límites geográficos. Paralelamente, se realizó una compilación bibliográfica del conocimiento existente sobre este par de especies. Esta información es relevante ya que estos murciélagos son consumidores especialistas de plantas pioneras en los procesos de sucesión y restauración ecológica, por lo que serán de gran ayuda en la regeneración de selvas y bosques perturbados ante el eminente cambio climático. Estas especies forrajean principalmente en zonas perturbadas, pero dependen en gran medida de la vegetación conservada donde perchan. Para preservar el beneficio ambiental que estos murciélagos ofrecen, es necesario conectar los parches de vegetación nativa adyacentes a los ambientes perturbados, y que en las zonas antropogenizadas se mantengan recursos alimenticios para promover que estos murciélagos visiten las áreas. De esta forma se mantendrán los procesos de sucesión ecológica de los paisajes modificados en donde las especies *Sturnira* habiten.

ABSTRACT

Mesoamerica, the Neotropical region comprising from Mexico to Panama, is considered a hotspot of biodiversity and a rich area in endemism. In this region there are widely distributed two species for the genus *Sturnira*, which is considered the most diverse of all frugivorous neotropical bats, but there are still controversies about their phylogenetic relationships and taxonomic limits among species. Recently it was postulated that some Mesoamerican subspecies should be recognized at species level, the first is *S. hondurensis*, a bat associated with template mountain forests, and the second is *S. parvidens*, associated with tropical lowland forests. Nevertheless, it is not known yet the evolutionary history of these species. Hence, the goal of this work was to analyze the evolutionary processes involved in the diversification of these two species, because they represent an excellent model of study because they inhabit in a region where several diversification processes have been recognized in many disparate taxa. Considering that these bats had a recent origin (*c.* 2.5 Ma), it is possible to recover much of their evolutionary history through phylogeographic (historical factors) and environmental niche (ecological factors) analyzes. To do so, phylogenetic relationships, level of genetic variation and genetic structuration, historical demography, as well as tests of niche similarity were analyzed in a comprehensive framework. Both species show resemblance in their evolutionary processes, for example, they were affected by severe past climatic changes that impacted their genetic diversity and genetic structuration. It promoted the genetic and ecological differentiation in each species of a lineage located in western Mexico. Besides, in this region was observed a more stable historical demography, likely as a consequence of the complex topography in the area that allowed the permanency of populations during intervals of climatic change. It is worth noting that the geographic features are the main source of differentiation in the montane species, whereas in the lowland species these processes are related with niche divergence in areas without apparent geographic barriers. These results suggest that despite existing similar biogeographic patterns, the processes that originated them are species-specific, and the biology of each taxon is determinant in the mechanism of biology evolution. Besides, results support that these Mesoamerican taxa are independent lineages, in addition to clarify its geographic limit ranges. In parallel, a bibliographic compilation was made in order to gather all the knowledge about these pair of species. This information is relevant because these bats are specialist consumers of pioneer plants in the successional processes and ecologic restoration, so that they will be of great help in the regeneration of perturbed vegetation in the face of impending climate change. These species mainly forages in perturbed areas, but they mainly depend of conserved vegetation where they roost. To preserve the environmental benefits that these bats offer, it is necessary to connect patches of native vegetation adjacent to perturbed areas, and to offer some alimentary resources in modified regions to promote that they visit the areas. In this way, the successional processes will remain in modified landscapes where the *Sturnira* species inhabit.

INTRODUCCIÓN GENERAL

Mesoamérica

En términos biológicos, Mesoamérica es considerada como una de las áreas más complejas y diversas del mundo (Bryson et al., 2011b; Daza et al., 2010; González et al., 2011; León-Paniagua et al., 2007; Ruiz-Sanchez y Ornelas, 2014). Su superficie es de ~2.5 millones de km^2 y abarca la porción de la región Neotropical situada entre México y Panamá (Arbeláez-Cortés et al., 2010; Bryson et al., 2011a; Castoe et al., 2009; Cavers et al., 2003). Los principales eventos que han moldeado su compleja biodiversidad se relacionan con la orogénesis de sus componentes y la historia de su dinámica climática. Dichos fenómenos crearon nuevos hábitats, corredores, barreras y oportunidades ecológicas que promovieron la diferenciación genética y fenotípica en diferentes tiempos y escalas espaciales (González et al., 2011; Gutiérrez-García y Vázquez-Domínguez, 2012; McCormack et al., 2008).

Su componente más antiguo es la Sierra Madre Oriental, que proporcionó hábitats terrestres desde finales del Cretácico y el Paleoceno (Graham, 1998); además desde el Paleoceno existieron periodos de actividad volcánica que formaron la Sierra Madre del Sur (Morán-Zenteno et al., 1999). Por otra parte, la Sierra Madre Occidental emergió durante el Oligoceno (Ferrari et al., 2005), y la Faja Volcánica Transmexicana tuvo sus orígenes en el Mioceno (Gómez-Tuena et al., 2005), después de que comenzaba la sedimentación continental de la Sierra Madre de Chiapas (Ferrusquía-Villafranca, 1998). Los levantamientos importantes más recientes se localizan en el sureste de México y Centro América: el Arco Volcánico centroamericano se formó en el Plioceno, el Arco Volcánico moderno de Chiapas durante los últimos 3 millones de años, y el levantamiento más

importante de las Cordilleras de Costa Rica y Panamá ocurrió en la transición Plioceno - Pleistoceno (Gutiérrez-García y Vázquez-Domínguez, 2013).

El levantamiento secuencial de la parte sureña de Mesoamérica propició la formación del Istmo de Panamá, un corredor biológico que permitió a múltiples especies expandir sus áreas de distribución entre Norte y Suramérica, dos continentes previamente aislados. Este intercambio comenzó desde el Mioceno, pero fue desde hace aproximadamente 2.8 millones de años (cuando culminó la formación del Istmo de Panamá) que la configuración de las biotas de ambos continentes cambió radicalmente (Gutiérrez-García y Vázquez-Domínguez, 2012; Navarro-Sigüenza et al., 2017; O'Dea et al., 2016).

Por otra parte, la formación del Istmo de Panamá interrumpió la comunicación entre los océanos Pacífico y Atlántico. Esto provocó una reorganización de las corrientes termohalinas, que aunado a las variaciones en la órbita terrestre, desencadenaron las fluctuaciones glaciales e interglaciales del Cuaternario (Bartoli et al., 2005; EPICA, 2004; Haug y Tiedemann, 1998; Hewitt, 2000). En este periodo geológico se agrupan las más recientes y mayores fases cíclicas de congelamiento y calentamiento global, y se divide en dos épocas: el Pleistoceno que comenzó hace *c.* 2.58 millones de años, y el Holoceno que inició hace *c.* 12,000 años (Gibbard et al., 2010). Es conocido que estas fluctuaciones glaciales e interglaciares han alterado la distribución y composición genética de la biota a nivel mundial, incluyendo las regiones tropicales (Hewitt, 2000).

De esta manera, la historia geológica de Mesoamérica y los cambios climáticos del Pleistoceno configuraron la biota mesoamericana, considerada como una mezcla de especies entre las regiones Neártica y Neotropical (Ríos-Muñoz, 2013) y el producto de

múltiples eventos de diversificación *in situ* (Bryson et al., 2011b; Gutiérrez-García y Vázquez-Domínguez, 2012; Hasbún et al., 2005; Hernández-Baños et al., 1995; León-Paniagua et al., 2007; Parra-Olea et al., 2012). Además, estos factores son causas importantes de el gran número de especies y taxones endémicos que presenta la zona, identificada como un *hotspot* de biodiversidad (Myers et al., 2000), tal como sucede para las especies de murciélagos del Nuevo Mundo (Ortega y Arita, 1998).

Género *Sturnira*

En el Neotrópico destaca la subfamilia de murciélagos frugívoros Stenodermatinae, por ser la más diversa en número de especies entre todas las subfamilias de murciélagos filostómidos (Owen, 1988). Un componente importante de esta gran diversidad está dado por el género *Sturnira*, considerado como el de mayor diversidad en toda la familia (Molinari et al., 2017).

Este género incluye especies de murciélagos pequeñas a grandes (10 – 68 g), que son fácilmente reconocibles por su cráneo relativamente corto y ancho, una hoja nasal bien desarrollada, un uropatagio muy reducido y peludo, y por carecer de cola (de la Torre, 1961; Velazco y Patterson, 2014, 2013).

Sturnira se distribuye desde México y las Antillas Menores hasta Argentina y se hipotetiza que sus 21 a 24 especies se agrupan en tres conjuntos: uno incluye especies que divergieron primero, y siguen otros dos clados denominados como A y B (Contreras-Vega y Cadena, 2000; Molinari et al., 2017; Sánchez-Hernández et al., 2005; Velazco y Patterson, 2014, 2013). En el clado A se localizan especies que generalmente habitan en

climas templados y montanos, y en el clado B especies asociadas a ambientes tropicales de tierras bajas (Velazco y Patterson, 2013; Villalobos y Valerio, 2002).

Se ha sugerido que este género divergió hace *c.* 12.6 – 15.9 Ma y que su centro de diversificación se localiza en los Andes (Velazco y Patterson, 2013). Estas especies cuentan con una limitada capacidad de dispersión, por lo que las especies mesoamericanas lograron invadir la región hasta después de la formación del Istmo de Panamá (Velazco y Patterson, 2013). Si bien este evento permitió que algunas especies colonizaran nuevas áreas y comenzaran a diversificar, es posible que los siguientes cambios climáticos afectaran los patrones de divergencia.

Ancestros de algunas especies del clado A lograron cruzar y establecerse en Mesoamérica y dieron origen a *Sturnira burtonlimi* y *S. mordax*, especies endémicas a los países de Costa Rica y Panamá, además de *S. hondurensis* que habita desde Nicaragua hasta México. Por otra parte, los ancestros de las especies del clado B que atravesaron el Istmo de Panamá dieron origen a *S. luisi* que habita desde Ecuador y alcanza su distribución más norteña en Costa Rica, y *S. parvidens* que se distribuye desde Costa Rica hasta México (Hernández-Canchola y León-Paniagua, 2017).

Debido a su reciente origen, su contrastante localización (zonas montanas *vs* tierras bajas) y a que se distribuyen ampliamente en la región, *S. hondurensis* y *S. parvidens* representan un buen sistema de estudio para indagar en sus procesos de diversificación. Por una parte, se puede investigar el efecto diferencial de la compleja orografía mesoamericana, además se puede analizar si las oscilaciones climáticas del Cuaternario pueden influir en los procesos de diversificación reciente.

Métodos de estudio

Una manera de analizar los procesos de diversificación reciente es por medio de la filogeografía. Esta disciplina se enfoca en la historia reciente de las especies, al analizar su variación genética y geográfica de linajes intraespecíficos o especies cercanamente relacionadas (Avise, 2000). Al analizar marcadores moleculares de varios individuos y comprender sus relaciones históricas en un contexto geográfico, es posible inferir la influencia de eventos geológicos o paleoecológicos asociados a la historia de las especies y sus ambientes (Arbeláez-Cortés, 2012).

Además de los eventos históricos, los procesos ecológicos también influencian la distribución de la variación genética entre poblaciones (Gutiérrez-Rodríguez et al., 2011), y son una pieza clave en muchos escenarios de especiación (Avise, 2000). Por ejemplo, una diferenciación significativa del nicho ambiental ocurre a la par de múltiples eventos de especiación (Warren et al., 2008). Es por ello que los estudios que combinan análisis filogeográficos y de nicho ecológico son esenciales para un mejor entendimiento de los factores implicados en la diferenciación dentro y entre poblaciones (Rodríguez-Gómez et al., 2013). Estos análisis son críticos para el entendimiento de los factores ecológicos en los procesos de formación de especies, también son útiles para la detección de linajes crípticos en taxones de amplia distribución que son morfológicamente conservados y para identificar límites de especies en estadios tempranos de especiación (Broennimann et al., 2012; Hu et al., 2016; Wiens, 2004).

En este contexto, el objetivo general de este trabajo fue analizar la influencia de los eventos históricos y ecológicos en la diversificación de dos especies mesoamericanas del género *Sturnira* que cuentan con distribuciones que ecológicamente son contrastantes. Para

ello, esta tesis se dividió de la siguiente manera: al inicio se presenta una Introducción general y al final se incluyeron la Discusión y las Conclusiones generales. Los Capítulos 1 y 3 analizan los procesos evolutivos de estas especies, y los Capítulos 2 y 4 consisten en una revisión bibliográfica sobre la biología e historia natural de los dos taxa. Finalmente, en la sección Anexo se incluye un trabajo derivado de la tesis, el cual consistió en el diseño de primers de microsatélites (ver en Discusión general).

CAPÍTULO 1.

Genetic and ecological processes promoting early diversification in the lowland Mesoamerican bat *Sturnira parvidens* (Chiroptera: Phyllostomidae)

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Giovani Hernández-Canchola y Livia León-Paniagua

Resumen

Con 22 especies, *Sturnira* es el género más diverso de murciélagos frugívoros Neotropicales. *Sturnira parvidens* habita en las áreas tropicales asociadas a altitudes bajas desde México hasta Centro América. El reconocimiento de este taxón al nivel específico fue reciente, y aún existen discrepancias acerca de sus límites geográficos y posición filogenética. Para identificar los procesos genéticos y ecológicos que posiblemente están involucrados en la diversificación y distribución actual de *S. parvidens*, evaluamos las relaciones filogenéticas, analizamos la filogeografía y demografía histórica, y evaluamos la divergencia / conservadurismo del nicho climático de este murciélago. Utilizamos datos de loci mitocondriales (citocromo b y la región hipervariable I del D-loop), y el gen nuclear activador de la recombinación 1, en 173 muestras de *S. parvidens* y 77 muestras de sus especies relacionadas. Realizamos análisis Bayesianos para inferir las relaciones filogenéticas y analizamos la estructura filogeográfica, la diversidad genética, los tiempos de divergencia y la demografía histórica. Los resultados indican que *Sturnira bakeri*, una especie que solo habita en el oeste de Ecuador, es el grupo hermano de *S. parvidens*. Estas especies divergieron *c.* 1.84 Ma, tienen una distribución disyunta, en la que se interpone *Sturnira luisi*. Al interior de *S. parvidens* hay dos haplogrupos con una distribución casi

alopátrida y que se limitan en la Sierra Madre del Sur, en la Vertiente del Pacífico mexicano. El tiempo de divergencia entre haplogrupos fue *c.* 0.423 Ma y detectamos señales de expansión demográfica. Además, analizamos 526 datos de ocurrencia de *S. parvidens* para analizar cambios en el nicho ambiental de esta especie. Encontramos señales de divergencia de nicho climático, principalmente en las variables de temperatura y estacionalidad. Posiblemente ambos procesos genéticos y ecológicos han moldeado la historia evolutiva de *S. parvidens*. A pesar de que múltiples oscilaciones climáticas ocurrieron durante el Pleistoceno, sólo las más intensas tuvieron un impacto en estos murciélagos. Además, la diferenciación ecológica evita el flujo genético, a pesar de no haber evidentes barreras geográficas al sur de la Sierra Madre del Sur. Concluimos que la especiación del género *Sturnira* fue promovida por la capacidad de este taxón para colonizar nuevos espacios geográficos y ambientales y formar grupos genéticamente estructurados cuando las poblaciones se encuentran aisladas.

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Genetic and ecological processes promoting early diversification in the lowland Mesoamerican bat *Sturnira parvidens* (Chiroptera: Phyllostomidae)

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ABSTRACT

With 22 species, *Sturnira* is the most speciose genus of frugivorous Neotropical bats. *Sturnira parvidens* inhabits lowland tropical areas from Mexico to Central America. The elevation of this taxon to species level was recent, and discrepancies with respect to its geographic limits and phylogenetic position continue to exist. In order to identify genetic and ecological processes likely involved in the diversification and current distribution of *S. parvidens*, we evaluated relationships, researched phylogeographic and demographic history, and tested the divergence/conservatism of the climatic niche of this bat. We used data from mitochondrial loci (*cytochrome b* and the *hypervariable D-loop region I*) and the nuclear *recombination activating gene 1*, in 173 samples of *S. parvidens* and 77 samples of related species. We performed Bayesian analyses to infer phylogenetic relationships and analyzed phylogeographic structure, genetic diversity, divergence times and historical demography. *Sturnira bakeri* is the sister group of *S. parvidens*, and inhabits Western Ecuador. The two species diverged *c.* 1.84 Ma, and their distributions are disjunct and separated by *Sturnira luisi*. Within *S. parvidens* there are two haplogroups with nearly allopatric distributions that are limited to the Sierra Madre del Sur, on the Mexican Pacific Slope. The divergence time between haplogroups was *c.* 0.423 Ma and we detected signals of demographic expansion. We also analyzed 526 occurrence data of *S. parvidens* to test for changes in environmental niche of this species. We detected signals of divergence of climatic niche, mainly in temperature and seasonality variables. Likely, both genetic and ecological processes have shaped the evolutionary history of *S. parvidens*. Despite many climatic fluctuations during the Pleistocene, only the most intense oscillations had an impact on these bats. In addition, ecological differentiation prevents admixture of genetic lineages that are in contact and lack apparent geographical barriers at the southern Sierra Madre del Sur. We concluded that speciation in *Sturnira* was promoted by this taxon's ability to colonize new geographical and environmental spaces and form genetically structured groups when populations become isolated.

1. Introduction

Geographic position, complex tectonic and orogenic history, climate patterns, and abrupt topography have acted together to generate high biodiversity in Mesoamerica (Bryson et al., 2011). This transitional area between biota from North and South America includes the Neotropical region from Mexico to Central America, and it has been considered one of the most intricate, complex, and diverse areas in the world (León-Paniagua et al., 2007; Myers et al., 2000). In addition to orogenic processes during the Miocene, two major biogeographic events are recognized as generators of biodiversity: the emergence of the Isthmus of Panama, which allowed species flow between previously isolated continents, and climatic oscillations during the Pleistocene, which modified climate, vegetation, and sea levels on a global scale (Gutiérrez-García and Vázquez-Domínguez, 2013).

Although the geographic position of Mesoamerica caused the effect of these climate changes to be less drastic than in areas near the poles, the biological consequences were heterogeneous and complex because its intricate topography affected climatic patterns both latitudinally and altitudinally (Moreno-Letelier and Piñero, 2009). One way to investigate the evolutionary processes

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that species experienced during this period of time is through phylogeographic studies. This discipline focuses on the recent history of species by analyzing the geographical and temporal variation of intra-specific lineages or of closely related species (Avise, 2000). While recent research has considered Mesoamerica, most of these works have focused on montane regions (e.g., Ornelas et al., 2013; Ramírez-Barahona and Eguiarte, 2013). Although there are some reports of genetic structure and early diversification processes in various lowland taxa, such as reptiles (Suárez-Atilano et al., 2014), birds (Arbeláez-Cortés et al., 2014), and mammals (Arteaga et al., 2012), there are few studies in Mesoamerican lowlands.

In addition to historical events, ecological processes also influence the distribution of genetic variation among populations (Gutiérrez-Rodríguez et al., 2011), and are key in most speciation scenarios (Avise, 2000). For example, significant environmental niche differentiation occurs in association with most speciation events (Warren et al., 2008). Studies that combine phylogeographical and ecological niche analyses are essential to better understand the factors implicated in population differentiation (Rodríguez-Gómez et al., 2013). These analyses are critical for understanding how ecological factors are linked to species formation, and are also useful in the detection of cryptic lineages in widespread morphologically conserved taxa, and for identifying species boundaries at early stages of speciation (Wiens, 2004a).

One genus of bats that contains morphologically conserved species is *Sturnira* (Chiroptera: Phyllostomidae). It is the most speciose genus of frugivorous Neotropical bats, comprising 22 species (Molinari et al., 2017; Velazco and Patterson, 2013) and includes three early-diverging Andean species (*S. aratathomasi*, *S. bidens*, and *S. nana*), a clade formed by 12 species that are usually found in montane forests (*S. adrianae*, *S. bogotensis*, *S. burtonlimi*, *S. erythromos*, *S. hondurensis*, *S. koopmanhilli*, *S. ludovici*, *S. magna*, *S. mordax*, *S. oporaphilum*, *S. perla*, and *S. tildae*; hereafter clade A), and seven species that inhabit lowland tropical forest and Caribbean islands (*S. angeli*, *S. bakeri*, *S. lilium*, *S. luisi*, *S.* new species 3, *S. paulsoni*, and *S. parvidens*; hereafter clade B). *Sturnira parvidens* inhabits Mesoamerican lowlands.

When initially described, *S. parvidens* was considered a subspecies of *S. lilium*. Nevertheless, molecular reviews of the *Sturnira* genus suggested that these two taxa deserved recognition as distinct species (Iudica, 2000; Velazco and Patterson, 2013). However, there is no consensus on inter-specific relationships within the clade of lowland *Sturnira* (Clare et al., 2011; Ditchfield, 2000; Hajibabaei et al., 2007; Iudica, 2000; Velazco and Patterson, 2013). There is also no consensus concerning the southern geographic boundary of *S. parvidens* (Ditchfield, 2000). Besides, *S. parvidens* is supposedly widespread throughout Mesoamerica, whereas many other species of *Sturnira* have localized geographic ranges (Velazco and Patterson, 2013).

The geographical and phylogenetic uncertainties of *S. parvidens* represent an excellent opportunity to study recent diversification processes in the Mesoamerican lowlands, since it was suggested that this bat evolved after the emergence of the Isthmus of Panama during the Pleistocene (Velazco and Patterson, 2013). In other words, it is an ideal candidate for exploring the effect of Quaternary climatic oscillations on the process of Neotropical biota formation. We performed phylogenetic and phylogeographic analyses based on DNA sequences of mitochondrial and nuclear molecular markers (including samples of *S. parvidens* from throughout its geographic range, and samples of all species in *Sturnira* clade B), and comparison of climatic niches, to determine the processes of diversification in this lowland Mesoamerican bat. Our main goals were (1) to clarify the phylogenetic position of *S. parvidens*, (2) to determine whether *S. parvidens* show genetic breaks due to the action of Pleistocene climatic oscillations in the Mesoamerican lowlands, and (3) to analyze the role of climatic niche conservatism or divergence in the speciation process.

2. Materials and methods

2.1. Taxon sampling and molecular protocols

We collected 54 specimens of *S. parvidens* in various states in Mexico following Mexico's wildlife legislation (SEMARNAT SGPA/DGVS/11606/08257/06724). All material is deposited in the Mammal Collection of the Zoology Museum, UNAM (Facultad de Ciencias – Universidad Nacional Autónoma de México, Mexico City, Mexico, MZFC-M). In the analyses we also included samples of *S. parvidens* and related species, to clarify the inter-specific position of *S. parvidens*, from other scientific collections: Instituto Politécnico Nacional – Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Durango, Mexico (CIIDIR-D); Louisiana State University, Museum of Natural Science, Baton Rouge (LSUMZ); Museo Nacional de Costa Rica, San José, Costa Rica (MNCR-M); Museum of Texas Tech University, Lubbock (TTU); and Royal Ontario Museum, Toronto, Canada (ROM). We also included 5 uncatalogued wing tissue samples that were collected in the field.

For total DNA, we followed a modified extraction protocol using NaCl and chloroform:isoamyl alcohol. Through polymerase chain reaction (PCR), we amplified the mitochondrial loci *cytochrome b* (*cyt-b*) and the *hypervariable D-loop region 1* (*D-loop*); and the nuclear *recombination activating gene 1* (*RAG1*) using the primers reported by Velazco and Patterson (2013). A negative control was included during each round of PCR. Each PCR had a final reaction volume of 12.5 μL and contained 7.325 μL of H_20, 1.25 μL Buffer [10x], 0.825 μL of dNTP's Mix [2 mM], 0.75 μL of $MgCl_2$ [25 mM], 0.625 μL of each primer [10 μM], 0.1 μL of Taq polimerase [5u/μL] (Vivantis Technologies Sdn. Bhd., Selangor, Malaysia), and 1 μL of DNA stock. The PCR profile included 3 min of initial denaturation at 95 °C, followed by 35 cycles of 30 s of denaturation at 95 °C, 1 min of annealing at 48–49 °C (*cyt-b*), 58 °C (*RAG1*), and 59 °C (*D-loop*); and 2 min for extension at 68 °C. Finally, we included a step of 8 min of final extension at 68 °C. With 1.5 μL of each PCR, we visualized these products through an electrophoresis in agarose gels with TAE [1x], stained with ethidium bromide. PCR products were cleaned with Exo-Sap and then were prepared to be read in an ABI 3730xl automatic sequencer.

The DNA sequences were edited and aligned using MEGA 6 (Tamura et al., 2013) and FINCHTV 1.4 (Patterson et al., 2004), conducting a visual inspection of all the sequences.

2.2. Phylogenetic analyses

To analyze the phylogenetic relationships between *S. parvidens* and related species, we included all the sequences available of genus *Sturnira* (Velazco and Patterson, 2013), and used *Vampyriscus bidens* as the out-group. Only in the case of *S. aratathomasi* did we combine the sequences of two different individuals (ROM 70874: *cyt-b*; and FMNH 189778: *D-loop*), following Velazco and Patterson (2013).

For the nuclear gene *RAG1* we obtained the allelic phases using the coalescent-based Bayesian method of the Phase algorithm (Stephens et al., 2001; Stephens and Donnelly, 2003) in DNASP 5.10 (Librado and Rozas, 2009). We employed 10,000 iterations, sampling data every 10 iterations, with a burn-in of 1000. We allowed recombination and set an output probability threshold of 0.9. We used the resulting highest probability haplotypes for further analyses.

We conducted five different phylogenetic analyses: one for each of the three molecular markers (*cyt-b*: n = 310; *D-loop*: n = 308;

RAG1: n = 539), plus two analyses of concatenated matrices (*cyt-b*/*D-loop*: n = 312; *cyt-b*/*D-loop*/*RAG1*: n = 312). Data were concatenated using one of the phased nuclear gene copies chosen at random for each individual (McCormack et al., 2011). In PARTITIONFINDER 2 (Lanfear et al., 2017, 2012) we found that the best scheme of partition of our dataset was *cyt-b*/*D-loop* + *RAG1*. Nevertheless, in JMODELTEST 2 (Darriba et al., 2015) we determined the best substitution model for each molecular marker, including *D-loop*: while this is mtDNA as *cyt-b*, both molecular markers have different mutation rates, and while *cyt-b* is a coding gene, *D-loop* is a control region in a non-coding area (Sbisa et al., 1997).

Bayesian analyses were performed in MRBAYES 3.2.3 (Ronquist et al., 2012) employing the MCMC algorithm. We used the substitution models calculated previously: *cyt-b*: GTR + I + Γ; *D-loop*: HKY + I + Γ; and *RAG1*: GTR + I + Γ. We used 3 hot and 1 cold chains, in two independent runs of 20 million generations, sampling data every 2000 iterations (40 million generations and a thinning of 4000 in the *RAG1* phylogeny). The final topology was obtained using a majority consensus of 50%, and considering a burn-in of 10%. We checked the convergence of our results and a good sampling (ESS > 200) in TRACER 1.6.

In MEGA 6 we calculated the genetic distances between lineages in *cyt-b* and *D-loop*, using the pairwise deletion option and the Kimura 2-parameter model (Kimura, 1980). We used these parameters with the goal of continuity and comparability with previous works (Baker and Bradley, 2006).

2.3. Genetic diversity and demographic analyses

In DNASP 5.10, the following genetic measures were calculated for each locus: number of segregating sites (S), number of haplotypes (h), haplotype diversity (Hd), nucleotide diversity (π), and average number of nucleotide substitutions per site between lineages (*dxy*).

To explore the demographic history of the species, we calculated Tajima's *D* (Tajima, 1989), Fu's *Fs* (Fu, 1997), *R2* (Ramos-Onsins and Rozas, 2002), raggedness index, τ value and the mismatch distributions (Rogers and Harpending, 1992). The significance of these values were assessed using the coalescent algorithm implemented in DNASP 5.10, using 1000 replicas. Since we detected signals of demographic expansion, we calculated the time from the expansion in the mitochondrial markers using the τ parameter (Rogers and Harpending, 1992): $\tau = 2ut$, where t is number of generations from the expansion, and $u = m_t\mu$. In u, m_t is the size of the sequence and μ is the mutation rate per site per year. We used specific mutation rates for *S. parvidens* that we calculated with the formula $T = dxy/2mu$ (Nei, 1987), where T is the time from divergence (see divergence times section), *dxy* is the average number of differences between two populations, and *mu* is the mutation rate. Once we had obtained the parameter t in τ, we transformed the number of generations to years using a generation time for *S. parvidens* of 7.5 months, considering a gestation period of 3.5 months (Taddei, 1976) and 4 months to reach reproductive maturity. The age of reproductive maturity is not known for *S. parvidens*, but was inferred from the reproductive pattern of this species (Sánchez-Hernández et al., 1986). This time has also been recorded in other bats of the Phyllostomidae family of similar size and diet, such as the *Carollia* genus (Molinari and Soriano, 2014).

2.4. Phylogeographic structure analyses

For each locus, we analyzed the geographic structure of the variable genetic sites in GENELAND (Guillot et al., 2012). We used this Bayesian method because it considers genetic data and their geographic coordinates to identify genetic discontinuities between populations and because GENELAND includes an option to work with haplotype data. We also used the option for codominant markers to analyze the allelic phases in *RAG1*. We tested the occurrence of different populations from 1 to 10, using 1 million generations with a thinning of 100, a true spatial model, uncorrelated genetic frequencies, and a value of 0.03° as coordinate uncertainty that correspond with the largest distance traveled by *S. parvidens* (Fenton et al., 2000). We did a burn-in of 1000, watched the convergence of the results over 10 independent runs, and chose the run with the highest likelihood value.

We tested for phylogeographic structure in the mitochondrial molecular markers. We calculated the values of genetic differentiation over all populations (G_{ST}), as well as the values of differentiation considering genetic distance (N_{ST}) using PERMUT (Pons and Petit, 1996). We tested the significance of the results with 10,000 permutations. N_{ST} values significantly greater than G_{ST} values were taken to corroborate a phylogeographic structure.

We analyzed hierarchical percentages of variation of previous results using a standard AMOVA in ARLEQUIN 3.5 (Excoffier and Lischer, 2010). We used a matrix of pairwise differences according to the Kimura 2-parameter model, using 10,000 permutations to test the significance of our results.

We generated three haplotype networks in NETWORK 5, using the Median Joining algorithm (Bandelt et al., 1999). Due to our relatively large data set, we followed the recommendations of the authors to visualize results. For the allelic phases in *RAG1*, we did not work with the unique allelic phases; and in *D-loop* we used the start contraction algorithm (set to 10). For the three loci we eliminated unnecessary median vectors using the MP option.

2.5. Divergence times

To estimate the divergence time between *S. parvidens* and its sister groups, as well as the time when its haplotypes originated, we constructed a calibrated species tree under a Bayesian approach in *BEAST, implemented in BEAST 2.4 (Bouckaert et al., 2014), using the mtDNA haplotypes and a phased sequence (n = 312). We unlinked the substitution and clock models between loci, and we linked the mitochondrial trees. We used molecular models for each molecular marker as in the Bayesian Inference, a lognormal uncorrelated clock for mitochondrial markers, a strict clock for the nuclear gene, and the Yule Speciation tree using a linear function for the Multi-Species Coalescent model.

We used three secondary calibration points that were calculated for the genus *Sturnira* by Velazco and Patterson (2013): the divergence time between *Sturnira* and other Stenodermatinae (14.25 Ma, CI [confidence interval]: 12.6–15.9); *Sturnira* clade A and *Sturnira* clade B (4.6 Ma, CI: 3.7–5.5); and the most recent common ancestor of *Sturnira* clade B (2.95 Ma, CI: 2.2–3.7). We constrained these groupings as monophyletic taxa as well as *S. parvidens* + *S. bakeri*. Two independent runs were made using 100 million generations, sampling data every 10,000 iterations. The convergence of both runs and the effective sample size were analyzed in TRACER 1.6, and the last 9000 trees of each analysis were combined in LOGCOMBINER 2.4. Finally, in TREEANNOTATOR 2.4, these results were summarized in a single maximum clade credibility tree considering a posterior probability limit of 0.5.

2.6. Comparison of climatic niches

Once we defined the geographic limits of *S. parvidens* and its haplogroups, we tested the niche similarity between them using the method proposed by Broennimann et al. (2012). This method includes a multivariate analysis of the environmental space that is gridded in *rxr* cells of unique environments, then an occurrence

density surface in environmental space is created using a kernel density method, considering the occupancy and availability of environments. We used these surfaces to calculate the amount of climatic niche overlap between genetic lineages, to test if the two niches are identical (niche equivalency test), and if they are more or less similar than expected under a null model of random distribution of points (niche similarity test) (Warren et al., 2008). We used 9 Bioclim variables at a resolution of 30 arc-seconds (Hijmans et al., 2005) that are important limiting factors of Neotropical bats (Stevens, 2011). Variables that characterized temperature were: annual mean, seasonality, maximum in the warmest month, and minimum in the coldest month and isothermality. Variables that characterized precipitation were: total annual, total in wettest month, total in driest month, and seasonality. For each haplogroup, we used the occurrence data available in VertNet, and we discarded the information from states where we found more than one genetic linage (Guerrero, Michoacán and Oaxaca in Mexico, and Costa Rica), due to uncertainty of its genetic membership. We also included the geographic information of all samples used for the genetic analyses. For definition of background environment, we used a buffer of 1° in the registers obtained. These analyses were performed in the R package ecospat, version 2.1.1 (Broennimann et al., 2016), and the niche tests were executed with 1000 iterations. To test whether climate divergence was retained in each haplogroup from the past or represents a more recent phenomenon, we also performed a niche conservatism/divergence test using the climatic information from two other past interglacial periods: the Last Interglacial (LI), and two climatic scenarios during the mid-Holocene, using projections from MH_{CCSM} and MH_{MIROC} (Hijmans et al., 2005). We estimated niche overlap and niche similarity/equivalence for those intervals, and compare the results with more recent times.

3. Results

3.1. Sample sizes

We analyzed data from 1 sample of *Vampyriscus bidens*, and 312 individuals of the genus *Sturnira*: 62 samples correspond to *S. aratathomasi*, *S. bidens*, *S. nana*, and species from clade A; 77 individuals corresponded to *S. angeli*, *S. bakeri*, *S. lilium*, *S. luisi*, *S.* new species 3, and *S. paulsoni*; and 173 samples to *S. parvidens*. All sequences are available in Genbank (Supporting Information, Table S1).

We obtained a total of 1140 bp for *cyt-b* (394 variable and 330 informative sites); 392 bp (entire data set, 166 variable and 133 informative sites) or 388 bp (only *S. parvidens* samples) in *D-loop*; and 1072 bp for *RAG1* (164 variable and 141 informative sites). Depending on the dataset, we obtained either 2604 or 2060 bp.

3.2. Phylogenetic analyses of Sturnira clade B

Sturnira clade B is composed of two clades (Fig. 1). One contains *Sturnira* new species 3, found in northern South America, mainly east of the Andes (in Peru, Ecuador, Venezuela, Guyana, Suriname, and French Guiana), and the island of Trinidad and Tobago, but also west of the Andes in Peru, as sister to all other species (*S. angeli*, *S. luisi* and *S. paulsoni*). *Sturnira angeli* (from Martinique, Dominica, Guadeloupe, and Montserrat), as sister to a clade composed by *S. luisi* (ranging from northern Costa Rica to northern Ecuador on the West Slope of the Andes, and Suriname), and *S. paulsoni* (from Grenada, St. Vincent and the Grenadines, and St. Lucia). The second clade includes *S. lilium* from Bolivia, Paraguay and Southern Brazil as sister to the clade composed by *S. bakeri* (found west of the Andes in Ecuador) and *S. parvidens* from tropical areas of Mexico to northern Costa Rica (Fig. 2).

With the mitochondrial concatenated matrix, we obtained a phylogeny that showed that *S. parvidens* clade is comprised of three groups: a branch with a high support value that corresponds to *S. bakeri;* a branch with intermediate support that contains samples of *S. parvidens* from the western slope of the Mexican Pacific (*S. parvidens* W); and several small branches that do not form a monophyletic group but are all found in eastern Mexico and Central America (*S. parvidens* E). Considering all three molecular markers, *S. bakeri* appears as a different species than *S. parvidens*, and we continue to obtain two lineages within this species (*S. parvidens* W and *S. parvidens* E). In addition, this last inference showed *S. aratathomasi* as the sister group of *Sturnira* clade B (Fig. 1).

The phylogenies obtained with each molecular marker displayed differences. The *cyt-b* estimation showed *S. bakeri* as the sister clade of *S. parvidens*; the *D-loop* showed *S. bakeri* as part of one branch within *S. parvidens* E, and the nuclear haplotypes formed a large group that included all of the samples from *Sturnira* clade B (Supporting Information, Fig. S1). Finally, in all but the nuclear phylogenetic inferences, we found two small clades inside *S. bakeri* that correspond with the samples from Northern and Southern Ecuador.

The genetic distance matrix showed small values among the species forming *Sturnira* clade B. In *cyt-b*, the values ranged from 1.36% (*S. luisi-S. paulsoni*) to 6.86% (*S. angeli-S. lilium*); and in *D-loop* from 3.65% (*S. luisi-S. paulsoni*) to 9.3% (*S. bakeri-S. new species 3*). The genetic distance between *S. bakeri* and *S. parvidens* from West and East were 3.67% and 3.03% in *cyt-b*, and 6.13% and 6.76% in *D-loop*, respectively, whereas between *S. parvidens* W and E, they were 1.18% in *cyt-b* and 3.68% in *D-loop* (Supporting Information, Table S2).

3.3. Genetic diversity and historic demography

We found 116, 135, and 161 haplotypes in *cyt-b*, *D-loop* and *RAG1*, respectively. The average percentage of variable sites in *cyt-b* was 6%, in *D-loop* was 13%, and in *RAG1* was 3%. In all loci and groupings, we detected high levels of haplotype diversity and low levels of nucleotide diversity. The average number of nucleotide substitutions per site between lineages in each molecular maker was similar to Kimura 2-parameter distances (Table 1; *cyt-b* = 0.0124; *D-loop* = 0.0367; *RAG1* = 0.0051).

Tajima's *D*, Fu's *Fs*, *R2* and raggedness indices showed higher and significant values of demographic expansion in *S. parvidens* E than in *S. parvidens* W (Table 2). The mismatch distributions showed unimodal distributions, similar to the expectation of a demographic model with population growth size, for all loci in *S. parvidens* E, and in all cases in *RAG1*. Nevertheless, in all other cases, mismatch distributions were multimodal (Supporting Information, Fig. S2).

3.4. Phylogeographic structure in S. parvidens

GENELAND Bayesian analysis indicated two genetic lineages within *S. parvidens* that corresponded with the groups found in the phylogenetic hypothesis. The probability assignment values were high, and the geographic boundaries between haplogroups were a bit different among mitochondrial and nuclear *loci*. The haplogroups were limited around the Sierra Madre del Sur (SMS), on the Pacific Slope of Mexico. To the north of SMS, there is an extension of the Trans-Volcanic Belt which keeps these lineages separated. However, to the south of SMS there are no evident barriers to gene flow

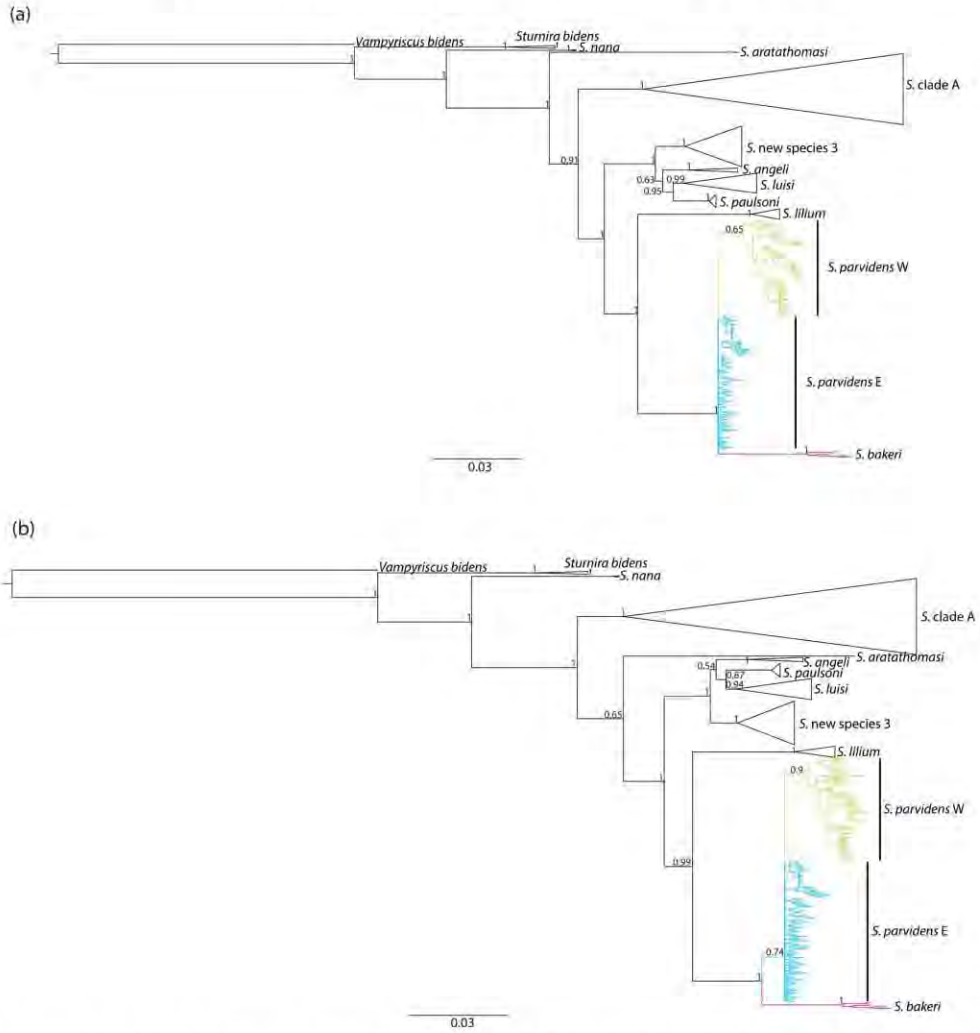

Fig. 1. Bayesian inferences that show the phylogenetic relationships within *Sturnira* clade B, showing the posterior probabilities at each node: (a) hypothesis with both mitochondrial loci, (b) hypothesis with three molecular markers (two mitochondrial and the nuclear loci). The height of enclosing triangles is proportional to the number of samples they contain. The colors indicate the following lineages: in green *S. parvidens* W, in blue *S. parvidens* E, and in pink *S. bakeri*.

or migration between the haplogroups, and in that area there are populations with haplotypes of both lineages (Fig. 3).

For the mitochondria, values of N_{ST} (*cyt-b* = 0.415 standard error, SE: 0.048; *D-loop* = 0.326 SE: 0.033) and G_{ST} (*cytb* = 0.044 SE: 0.021; *D-loop* = 0.043 SE: 0.021) indicated overall genetic differentiation across populations. In both cases, N_{ST} values were significantly higher than G_{ST} ($p < 0.01$), suggesting phylogeographic structure among *S. parvidens* populations.

This East-West division was corroborated by the AMOVA (Table 3). In *cyt-b*, the higher variation percentage was found between the two lineages (58.64%), while 42.1% was found within populations. However, in *D-loop*, higher variation was found within populations (56.18%) than between lineages (40.64%).

The mitochondrial networks recovered the East-West haplogroups, whereas the nuclear network showed some shared alleles between lineages. Nonetheless, few nuclear alleles are found only in the Western lineage, while many alleles were restricted to the Eastern lineage (Fig. 3).

3.5. Divergence and expansion times

The species tree obtained showed that *S. bakeri* diverged from *S. parvidens* during the Early Pleistocene *c.* 1.84 Ma (95% CI: 2.553–1.179) and haplogroups W and E diverged in the Middle Pleistocene, *c.* 0.423 Ma (95% CI: 0.586–0.268).

The specific substitution rates calculated over all sites for *S. parvidens* were *cyt-b* = 0.0147 s/s/Ma (95% CI: 0.0106–0.0233); *D-loop* = 0.0434 s/s/Ma (95% CI: 0.0313–0.0685); and *RAG1* = 0.0060 s/s/Ma (95% CI: 0.0043–0.0094). The time since expansion began ranged from 192,397 to 53,415 years ago in *S. parvidens* W; and from 140,638 to 43,761 years ago in *S. parvidens* E (Table 2).

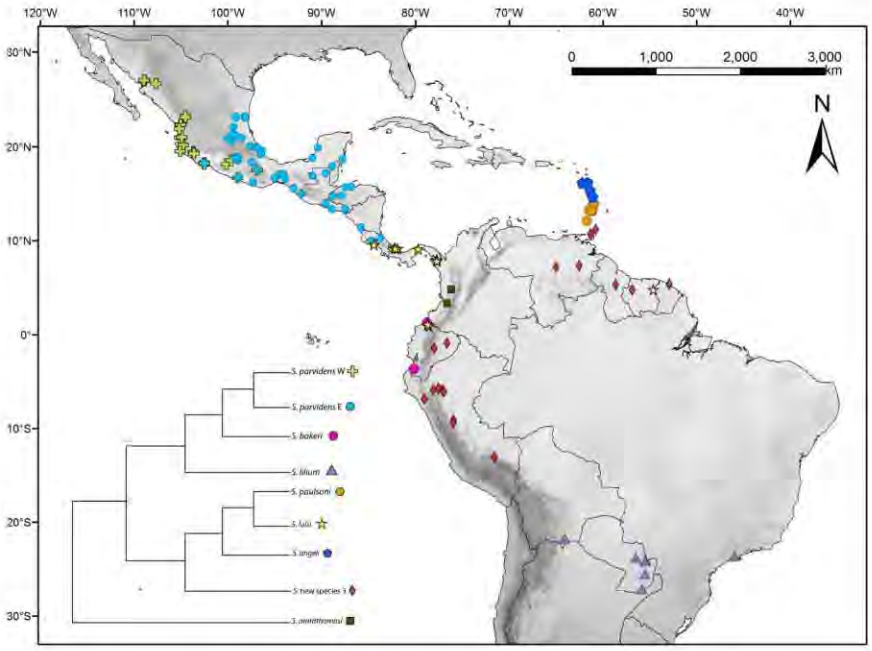

Fig. 2. Geographic distribution of samples of *Sturnira* clade B (*sensu* Velazco and Patterson, 2013) used in this work. Note that *S. luisi* interrupts the distribution between sister lineages *S. parvidens* and *S. bakeri* and is sympatric with both lineages at its range limits.

Table 1
Results of genetic diversity analyses for each molecular marker, for haplogroups W and E, and for *S. parvidens* as a whole. See text for details.

Loci	Taxa	n	S	h	Hd	Hd(sd)	π	π(sd)	dxy
cyt-b	*S. parvidens* W	73	65	50	0.981	0.007	0.00654	0.00041	
1140 bp	*S. parvidens* E	99	72	72	0.979	0.006	0.00326	0.0002	
	S. parvidens	172	118	116	0.99	0.003	0.00838	0.00026	0.0124
D-loop	*S. parvidens* W	73	57	59	0.993	0.004	0.02612	0.00104	
388 bp	*S. parvidens* E	100	50	76	0.988	0.006	0.01659	0.00078	
	S. parvidens	173	72	135	0.995	0.002	0.02811	0.00076	0.0367
RAG1	*S. parvidens* W	134	29	43	0.942	0.01	0.00349	0.00021	
1072 bp	*S. parvidens* E	188	48	86	0.979	0.004	0.00555	0.00015	
	S. parvidens	322	56	116	0.976	0.003	0.00496	0.00013	0.0051

Table 2
Demographic results for *S. parvidens*, and for each haplogroup within the species.

Loci	Group	*D*	*Fs*	*R2*	*r*	τ	Generations from expansion			Years from expansion		
							Mean	H95-L	H95-H	Mean	H95-L	H95-H
cyt-b	West	**−1.506**	**−39.1102**	**0.0524**	0.0059	4.537	134957	85464	186905	84348	53415	116816
	East	**−2.4089**	**−96.6563**	**0.0231**	**0.0338**	3.717	110565	70018	153125	69103	43761	95703
	Total	**−1.7556**	**−136.065**	**0.0381**	**0.0088**	5.183	154173	97633	213518	96358	61021	133448
D-loop	West	−0.5488	**−50.0729**	0.0849	0.0061	7.479	222275	140760	307835	138922	87975	192397
	East	−1.2279	**−34.5082**	0.0623	0.0075	5.467	162479	102893	225021	101549	64308	140638
	Total	−0.6854	**−34.4167**	0.074	0.0023	7.75	230330	145861	318989	143956	91163	199368
RAG1	West	−0.8606	**−31.3269**	0.0639	**0.0105**	2.536	197856	125296	274016	123660	78310	171260
	East	**−0.8783**	−89.823	0.0614	**0.0178**	5.951	464291	294022	643008	290182	183764	401880
	Total	**−1.1783**	−144.235	**0.0471**	**0.0131**	4.887	381279	241453	528042	238299	150908	330026

Boldface numbers indicate significant values ($p < 0.05$ in *D*, *R2* and *r*; and $p < 0.02$ in *Fs*). The mean and intervals of time divergence between haplogroups were used to calculate the time since expansion began. H95-H indicates the Highest Posterior Density Interval of 95%, and H95-L the lower interval.

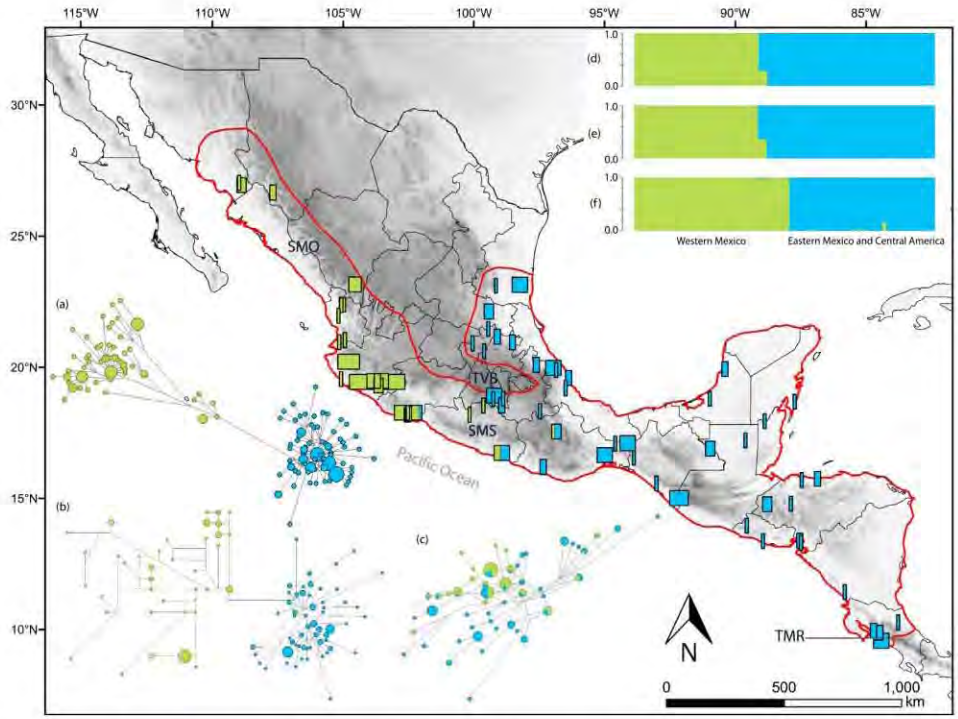

Fig. 3. Phylogeographic structure in *Sturnira parvidens*. The green color shows the haplogroup W, and blue haplogroup E. The map shows the distribution of each genetic group, and the bar size is proportional to number of samples per locality. The red line represents the proposed geographic range of this species. At the bottom left, the networks for each molecular marker: (a) *cyt-b*, (b) *D-loop*, and (c) *RAG1*. The circle size is proportional to the frequency of haplotypes or alleles, and the line length to the number of mutations. At the top right, the assignment probabilities for each individual to the lineages: (d) *cyt-b*, (e) *D-loop*, and (f) *RAG1*. SMO: Sierra Madre Occidental; TVB: Trans-Volcanic Belt; SMS: Sierra Madre del Sur; TMR: Talamanca Mountain Range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Results of the analyses of molecular variance (AMOVA) performed on the haplogroups W and E in *S. parvidens* using the mtDNA markers.

Molecular marker	Source of variation	Percentage of variation	Fixation index
cyt-b	Among groups	58.64	**0.58643**
	Among populations within groups	−0.74	−0.01791
	Within populations	42.1	**0.57903**
D-loop	Among groups	40.64	**0.40639**
	Among populations within groups	3.18	**0.05355**
	Within populations	56.18	**0.43818**

Boldface numbers indicate significant values ($p < 0.05$).

3.6. Niche overlap, equivalency and similarity

We initially obtained 665 occurence records from VertNet and our data. After discarding records within 1 km of each other, we analyzed 526 occurrence data (*S. parvidens* W = 192, and *S. parvidens* E = 334). The first two components of the PCA performed for niche comparison (Fig. 4 and Supporting Information, Fig. S3) accounted for 71% of the total environmental variation within the study area. The overlap metric was close to 0 (D = 0.01), and tests of equivalency ($p = 1$) and similarity ($p = 0.59$ and 0.58) indicated that the niches of the haplogroups were neither equivalent nor more similar than expected by chance, proving that there is no significant climatic niche conservatism between haplogroups (Di Cola et al., in press). Despite the haplogroups not having colonized all climatic conditions available in the study area (niche unfilling = 63.26%), niche differentiation is due to the lineage's ability to expand into novel climates (niche expansion = 15.12%; Table 4). The Western haplogroup is able to inhabit more extreme temperatures, particularly areas with the coldest temperatures during the coldest month. The seasonality in both temperature and precipitation also influenced this differentiation of climatic niches (Supporting Information, Fig. S4). Nevertheless, the haplogroups did not show climatic expansion with respect to isothermality and other precipitation variables (total annual, during the wettest and driest month; niche expansion = 0%).

The niche conservatism/divergence test using the climatic information from LI, MH_{CCSM} and MH_{MIROC} showed evidence of niche divergence (D = 0.01; equivalency and similarity test with $p > 0.05$, in all cases), and signals of an upward niche differentiation over time (percentage of niche expansion LI = 11.87; MH_{CCSM} = 11.54; MH_{MIROC} = 15.05; and present = 15.12).

4. Discussion

Molecular information is important in bats of the genus *Sturnira* because the relationships of these species cannot be clarified using a morphological perspective alone (Iudica, 2000; Pacheco and Patterson, 1991). In addition, morphological variation within the genus is subtle, and in some cases the characters used to diagnose

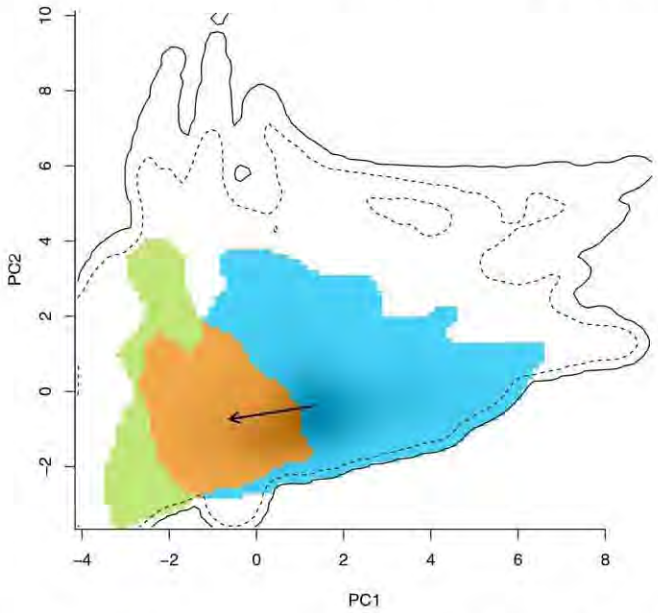

Fig. 4. Climatic niche of *Sturnira parvidens* along the first two axes of the PCA. In green the Western haplogroup, in blue the Eastern haplogroup, and in orange the space shared by both lineages. The solid and dashed contour lines illustrate 100% and 50% of the available environment. Grey shading shows the density of the occurrence data. The arrow represents how the center of the niche has changed between haplogroups East and West. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Percentages of expansion, stability and unfilling between the climatic niches of the haplogroups West and East.

Climatic variable	Expansion	Stability	Unfilling
Temp. annual mean	2.04	97.96	0.00
Temp. maximum warmest month	1.06	98.94	0.00
Temp. minimum coldest month	2.15	97.85	0.00
Temp. seasonality	1.86	98.14	0.00
Isothermality	0.00	100.00	0.84
Precip. total annual	0.00	100.00	29.82
Precip. total wettest month	0.00	100.00	10.98
Precip. total driest month	0.00	100.00	71.41
Precip. seasonality	6.08	93.92	58.33
9 variables	15.12	84.88	63.26

different species have proven to be inconsistent (Jarrín-V and Clare, 2013).

Herein, we reported some relationships between the species of genus *Sturnira* that are different to a previous hypothesis based in seven nuclear and three mitochondrial loci, that represent the major analysis about the evolution and biogeography of New World noctilionoid bats (Chiroptera: Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, and Thyropteridae) (Rojas et al., 2016). Nevertheless, in the particular case of the samples of the genus *Sturnira*, the authors constructed their hypothesis including only one mitochondrial marker in the majority of these species (Rojas et al., 2016). On the other hand, the hypothesis of Velazco and Patterson (2013) included three mitochondrial and two nuclear loci and various individuals per species. These kind of markers and the number of samples helped to clarify with a better resolution the phylogenetic relationships inside this genus.

It is important to mention that Rojas et al. (2016) showed that changes in speciation rates in phyllostomid bats are not dependent on any geological period but are clade-dependent. Our divergences are related with important climatic changes, and we suggest that lineage accumulation plus Pleistocene climatic oscillations molded together the diversification and distribution of *Sturnira* clade B and haplogroups within *S. parvidens*. For example, the Quaternary changes allowed multiple migrations, and it was probed that dispersal is important in the evolutionary history of these groups of bats (Rojas et al., 2016).

4.1. A South American origin

Our data corroborate the monophyly of *Sturnira* clade B, a group of species that usually inhabits lowland tropical ecosystems. These species had a highland ancestor that inhabited montane forest in the Andes (Velazco and Patterson, 2013). This ecological change may have been accompanied by the fixation of a character that allowed these species to survive in new environments. For example, the molar cusp patterns in phyllostomid bats correspond with their food habits (de la Torre, 1961), and in all species of clade B, the lingual cusps of lower molars are well defined and separated by a deep notch. This morphology could represent a character acquired with tropical lowlands diets.

Our phylogenies differ from a previous one constructed with five molecular markers, but fewer samples (Velazco and Patterson, 2013). In this previous study, *S. aratathomasi* was one of the three species that first diverged from the core of the genus; however, we recovered *S. aratathomasi* as the sister group of clade B. Our result is similar to an analysis based on partial *cyt-b* and morphological data (Iudica, 2000), but we are uncertain about the phylogenetic position of *S. aratathomasi* because both studies relied on a sample comprised of DNA from two individuals.

As previously suggested, the two species that inhabit the West Indies (*S. angeli* and *S. paulsoni*) do not form a monophyletic group (Iudica, 2000; Velazco and Patterson, 2013). Geographically, *S. angeli* is the farthest species from the mainland, and originated

before *S. paulsoni*. It has been suggested that both species originated from mainland populations in two independent migrations during glacial cycles of the Pleistocene, thanks to the changes in the level sea that favored the connection between continental and island habitats. This is relevant in bats like *Sturnira* that are seemingly averse to or incapable of crossing open water (Iudica, 2000; Velazco and Patterson, 2013).

Sturnira luisi was originally described as a species that ranges from Costa Rica to northern Peru to the West of the Andes and has straight zygomatic arches (Davis, 1980). However, we found one haplotype in Suriname. Because this species is very recent (Velazco and Patterson, 2013) this haplotype most likely the consequence of incomplete lineage sorting. Nevertheless, samples from Colombia, Venezuela, Guyana, Suriname and French Guiana are needed to reject other hypotheses, such as genetic flow or range expansion.

Another species with straight zygomatic arches is *S. bakeri* (Velazco and Patterson, 2014). We found a possible geographic structure within this species, with a division between northern and southern populations in Ecuador that have a distance value of 1.21 (*cyt-b*), similar to the value between haplogroups of *S. parvidens* (1.18). We found haplotypes of *S. bakeri* in northwestern Ecuador, an area where it is sympatric with *S. luisi* and where both linages have their boundaries. The southern limit of *S. bakeri* is likely northern Peru (see also Velazco and Patterson, 2013), as was previously suggested for *S. luisi* (Davis, 1980). Nevertheless, Jarrín-V and Clare (2013) noted that the presence of straight zygomatic arches is an inconsistent character in Ecuadorian *Sturnira* lineages. For that reason, it is necessary to re-evaluate samples that have been genetically identified as *S. luisi* and *S. bakeri*, to establish diagnostic characters that better define both species. *Sturnira* new species 3 is located in the Amazon region and could have colonized west of the Andes via the Huancabamba Deflection in northern Peru, like other phyllostomid bats (Hoffmann and Baker, 2001; Patterson et al., 1992). It is possible that this species includes wide morphological variation that may obscure its future description, as has been reported in other *Sturnira* species (Jarrín-V and Clare, 2013).

Our results indicate with high probability values that *S. lilium* is the sister group of *S. bakeri* + *S. parvidens*. The origin of these species is probably related to the orogeny of the Andes. The Northern Andes reached their maximum heights just 2 Ma, and this process happened quickly, not gradually (Gregory-Wodzicki, 2000).

The sister taxon of *S. bakeri* is *S. parvidens*. A close relationship between taxa from western Ecuador and Mesoamerica is a common pattern among phyllostomid frugivorous bats (e.g., Larsen et al., 2007; Patterson et al., 1992; Velazco and Patterson, 2008). Nonetheless, in some cases *S. bakeri* appears as an internal branch of *S. parvidens*, suggesting that *S. bakeri* colonized Western Ecuador from a population of *S. parvidens*. It has been suggested that the migration from Mesoamerica to West of the Central Andes occurred due to glacial cycles during the Pleistocene: changes in temperature and moisture in the Quaternary allowed the connection of biota between both areas, while the modern climate fragmented those previous distributions. The divergence time between species (*c.* 1.84 Ma ± 2.553 – 1.179) is consistent with age of divergence reported in the multilocus work of Rojas et al. (2016), and coincides with one of the pulses of the Great American Biotic Interchange (GABI-2), during which time more taxa of mammals migrated southward than northward (Woodburne, 2010). This hypothesis suggests first migration from South America towards Mesoamerica, then later re-colonization of South America.

4.2. Diversification in Mesoamerica

Sturnira parvidens was considered a subspecies of *S. lilium*; nevertheless, it has been recognized as an independent species since Iudica (2000) and Velazco and Patterson (2013). We agree with this hypothesis because there are many differences between these taxa, from geographical and morphological differences (Sánchez-Hernández and Romero-Almaraz, 2003) to genetic distance values, and they represent independent lineages. Nonetheless, the geographic boundaries of *S. parvidens* have not been clarified (Iudica, 2000), possibly due to the unexplained morphological variation of *S. bakeri*, *S. luisi*, and *S.* new species 3 (Jarrín-V and Clare, 2013).

Our analyses with a large data set showed that the *S. parvidens* lineage is found from Sonora, Mexico on the Pacific Slope, and Tamaulipas, Mexico on the Gulf coast southward, including the Yucatan Peninsula, to northern Costa Rica. Its southern limit coincides with the Talamanca Mountain Range and with the northern limits of *S. luisi*. The northern lowland areas of the Talamanca Mountains allow contact between these two species. Ditchfield (2000) recognized that the geographic barriers that divide clades in lowland *Sturnira* species are not absolute, therefore historical, ecological, or behavioral agents could help maintain their separation (Avise, 2000).

Our phylogeographic pattern is similar to those reported in other lowland species, as in the boa *Boa constrictor imperator* (Suárez-Atilano et al., 2014), the nine-banded armadillo *Dasypus novemcinctus* (Arteaga et al., 2012), and in the bird *Passerina leclancherii* (Arbeláez-Cortés et al., 2014). In spite of there being no obvious current barriers in the lowlands, there are many taxa that have genetic breaks in the area (Arbeláez-Cortés et al., 2014). On Mexico's Pacific Slope, the Sierra Madre Occidental, the Trans-Volcanic Belt and the SMS intersect, generating an abrupt and heterogeneous topography that has promoted diversification events (Becerra and Venable, 2008). This feature has allowed many taxa at different times to become isolated, according the biology of each species. For that reason, similar genetic patterns may have occurred at different geological times by different processes. For example, the phylogeographic patterns mentioned were a consequence of different historical events such as the divergence during the Neogene (Suárez-Atilano et al., 2014), two independent migrations during the GABI (Arteaga et al., 2012), or diversification processes during the Pleistocene (Arbeláez-Cortés et al., 2014). While there are stronger signals of demographic expansion on the east side, the heterogeneous topography in western Mexico probably allowed the persistence of multiple lowland populations in which demographic growth was less evident.

Pleistocene climate changes are strongly suspected to have promoted the contraction and isolation of previous continuous populations, stimulating allopatric divergence (Jaramillo-Correa et al., 2008). Palynological, fossil, and phylogeographic research in Mesoamerica suggest that during glacial-interglacial periods, tropical lowland biota migrated southward during cold periods, and they returned northward during warm inter-cycles (Guevara-Chumacero et al., 2010; Poelchau and Hamrick, 2013). Because Pleistocene climatic changes were cyclical, there were ample opportunities to diverge (Barber and Klicka, 2010). However, the cycles that promoted the differentiation must have been severe if they were to ensure complete isolation and maintenance of distinct populations in subsequent cycles (Jaramillo-Correa et al., 2008). This is consistent with the information that we obtained for *S. parvidens*.

The magnitude and frequency of glacial cycles were changing just as haplogroups E & W were diverging (*c.* 0.423 Ma ± 0.586 – 0.268). The glacial MIS-12, matched in intensity by only one previous cycle, ended 0.424 Ma (Lisiecki and Raymo, 2005), and after MIS-12, the glacial cycles fell into a more predictable 100,000-year cycle, and a clear relationship between greenhouse gases and climate emerged (EPICA Community Members, 2004). This period may have promoted a strong division and isolation of *S. parvidens* populations that initiated their genetic

differentiation, and this signal was not erased in the following cycles.

Despite recent divergence time between haplogroups, there is evidence of climatic differentiation. This is important in the process of formation of new species, since historical colonization ability and environmental suitability are important factors that shape the distribution of species in time and space (Di Cola et al., in press).

The most important variables related to the current change in climatic niche were related to temperature and seasonality, both of which are characteristics that could describe the nature of the tropical dry forest in Western Mexico. *Sturnira parvidens* feeds and roots on Mesoamerican plant species, and it has been shown that temperature does not affect their growth, because some plants are mainly affected by rainfall (Brienen et al., 2010). On the other hand, seasonality (temporal resource availability) has been reported as an important variable in the process of adaptation due to it is relationship with stress tolerance (Sher et al., 2004). We suspect that the main change in the climatic diverge between haplogroups is not related with the availability of resources (because plants depend more of water), and it may be related with changes in the physiological tolerance that allow to the haplogroup W to survive in colder and more seasonal places such as the environments available in the tropical dry Mexican forest. This region is relevant in the evolutionary processes of many Mexican mammals; for example, the majority of Mexican endemic genera are found in Western Mexico (Ceballos et al., 2005).

In the case of similar phylogeographic structure detected in the armadillo *D. novemcinctus*, there is no clear differentiation of niches between lineages, and it was calculated that the niche of Eastern populations contains much of the Western niche. The genetic consequences of this particular case showed a mixture of individuals, where many East-to-West (but not West-to-East) migrants were detected (Arteaga et al., 2011). Conversely, our results show a clear geographic division of haplogroups, which is consistent with the climatic differentiation detected. The cases of the armadillo and *S. parvidens* demonstrate that the degree to which ecological niches are conserved could allow or restrict the genetic flow, carrying evolutionary implications that include the role of ecology in the speciation process (Warren et al., 2008).

Niche conservatism is the tendency of species to retain similar ecological niches over evolutionary time scales (Wiens, 2004b), and we observed an upward niche divergence through time. We do not kwon when and how this climatic differentiation started, but it has been gradual and constant, at least in the recent history of these haplogroups, and it could be the consequence of the genetic variability and the adaptation to new exposed conditions (Wiens, 2004b). Our results suggest that both Pleistocene climatic oscillations and the ecological divergence have played an important role in promoting and maintaining the differentiation of haplogroups of *S. parvidens*. This genetic and ecological pattern may be an intermediate step towards the formation of new species (Avise, 2000).

The Neotropics are known for their high biodiversity and endemism (Myers et al., 2000), and the currently recognized 22 *Sturnira* species include early-diverging and recently diverged species, which have differentiated since the Late Miocene due to various geological and climatic processes (Velazco and Patterson, 2013). In this work, we investigated the evolutionary history of *S. parvidens* and related species, and they seem to be experiencing intermediate steps towards formation of new species. The phylogenetic component, the ability of these bats to colonize new areas, to form genetically structured groups, and the ecological differentiation, have helped make *Sturnira* the most speciose of all New World leaf-nosed bats genera.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.06.015.

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SUPPORTING INFORMATION

Genetic and ecological processes promoting early diversification in the lowland Mesoamerican bat *Sturnira parvidens* (Chiroptera: Phyllostomidae)

Giovani Hernández-Canchola and Livia León-Paniagua

Additional file 2

Table S2. Genetic distance matrix for species of the genus *Sturnira* using Kimura 2-parameters model. Above the diagonal the values for *D-loop*, and below the diagonal the values for *cyt-b*.

	Vamp	S_bid	S_nan	S_ara	S_hon	S_bur	S_lud	S_opo	S_til	S_per
Vamp		0.1638		0.1714	0.1999	0.2075	0.1998	0.1993	0.2477	0.2062
S_bid	0.1420			0.1146	0.1152	0.1262	0.1202	0.1410	0.1885	0.1345
S_nan	0.1421	0.0870								
S_ara	0.1562	0.1148	0.1035		0.1091	0.1119	0.1006	0.1077	0.1616	0.1107
S_hon	0.1542	0.1029	0.1030	0.0984		0.0581	0.0478	0.0671	0.1493	0.0762
S_bur	0.1542	0.1006	0.0866	0.0940	0.0414		0.0582	0.0609	0.1455	0.0895
S_lud	0.1449	0.1051	0.0857	0.0868	0.0556	0.0486		0.0551	0.1496	0.0827
S_opo	0.1538	0.1059	0.0920	0.0925	0.0561	0.0420	0.0437		0.1592	0.0865
S_til	0.1572	0.1133	0.0924	0.0807	0.0908	0.0767	0.0729	0.0801		0.1289
S_per	0.1492	0.0912	0.0811	0.0822	0.0674	0.0603	0.0610	0.0665	0.0657	
S_koo	0.1489	0.0997	0.0872	0.0807	0.0781	0.0639	0.0661	0.0644	0.0669	0.0610
S_mor	0.1529	0.0994	0.0869	0.0819	0.0667	0.0454	0.0505	0.0549	0.0591	0.0520
S_mag	0.1573	0.1258	0.1089	0.1016	0.0807	0.0711	0.0661	0.0771	0.0809	0.0659
S_bog	0.1491	0.0998	0.0975	0.0924	0.0780	0.0716	0.0530	0.0719	0.0663	0.0634
S_ery	0.1613	0.1094	0.0922	0.0849	0.0839	0.0668	0.0700	0.0751	0.0711	0.0538
S_ns3	0.1392	0.0936	0.0767	0.0599	0.0691	0.0651	0.0638	0.0633	0.0700	0.0636
S_ang	0.1521	0.0925	0.0801	0.0655	0.0830	0.0781	0.0726	0.0728	0.0778	0.0718
S_lui	0.1445	0.0950	0.0732	0.0670	0.0793	0.0716	0.0675	0.0718	0.0749	0.0654
S_pau	0.1459	0.0891	0.0747	0.0621	0.0729	0.0655	0.0646	0.0648	0.0748	0.0661
S_lil	0.1629	0.1062	0.0939	0.0882	0.0788	0.0762	0.0724	0.0720	0.0794	0.0741
S_bak	0.1560	0.1145	0.0870	0.0848	0.0874	0.0848	0.0765	0.0794	0.0914	0.0741
S_parE	0.1572	0.1052	0.0897	0.0773	0.0763	0.0764	0.0721	0.0741	0.0796	0.0752
S_parW	0.1601	0.1082	0.0948	0.0833	0.0806	0.0783	0.0780	0.0778	0.0818	0.0774

Table S2. Cont.

	S_koo	S_mor	S_mag	S_bog	S_ery	S_ns3	S_ang	S_lui	S_pau	S_lil
Vamp	0.1889	0.1863	0.1929	0.2081	0.2024	0.2014	0.2036	0.1837	0.1801	0.1715
S_bid	0.1579	0.1277	0.1198	0.1352	0.1612	0.1294	0.1271	0.1243	0.1119	0.1150
S_nan										
S_ara	0.1218	0.1208	0.0944	0.1366	0.1166	0.1024	0.1155	0.1059	0.0903	0.0940
S_hon	0.0966	0.0669	0.0849	0.1047	0.1012	0.0922	0.0955	0.0829	0.0670	0.0846
S_bur	0.1184	0.0900	0.0931	0.1208	0.1162	0.1063	0.1120	0.0949	0.0917	0.1006
S_lud	0.1129	0.0823	0.0808	0.1209	0.1105	0.1149	0.0991	0.0930	0.0798	0.1026
S_opo	0.0999	0.0827	0.0963	0.1424	0.1243	0.1211	0.1125	0.0963	0.0889	0.1001
S_til	0.1632	0.1311	0.1378	0.1484	0.1286	0.1494	0.1535	0.1467	0.1366	0.1363
S_per	0.0840	0.0610	0.0665	0.1216	0.0969	0.0968	0.0855	0.0753	0.0660	0.0848
S_koo		0.0598	0.0893	0.1312	0.1174	0.1122	0.1014	0.0981	0.0997	0.0929
S_mor	0.0440		0.0683	0.0975	0.0882	0.0902	0.0901	0.0795	0.0700	0.0821
S_mag	0.0684	0.0600		0.1045	0.0984	0.0928	0.0833	0.0855	0.0727	0.0915
S_bog	0.0618	0.0557	0.0567		0.1222	0.1099	0.1199	0.1172	0.1117	0.0972
S_ery	0.0636	0.0633	0.0673	0.0586		0.1259	0.1348	0.1191	0.1132	0.1257
S_ns3	0.0585	0.0565	0.0733	0.0550	0.0697		0.0630	0.0634	0.0478	0.0756
S_ang	0.0688	0.0678	0.0832	0.0671	0.0759	0.0224		0.0597	0.0483	0.0677
S_lui	0.0657	0.0639	0.0765	0.0617	0.0727	0.0154	0.0218		0.0365	0.0592
S_pau	0.0616	0.0599	0.0728	0.0596	0.0722	0.0157	0.0224	0.0136		0.0603
S_lil	0.0712	0.0683	0.0814	0.0710	0.0712	0.0587	0.0686	0.0591	0.0564	
S_bak	0.0823	0.0796	0.0954	0.0869	0.0779	0.0565	0.0661	0.0584	0.0593	0.0666
S_parE	0.0679	0.0709	0.0927	0.0745	0.0745	0.0454	0.0545	0.0506	0.0485	0.0545
S_parW	0.0729	0.0770	0.0911	0.0758	0.0738	0.0482	0.0559	0.0517	0.0498	0.0609

Table S2. Cont.

	S_bak	S_parE	S_parW
Vamp	0.2006	0.1801	0.1850
S_bid	0.1357	0.1315	0.1304
S_nan			
S_ara	0.1164	0.1119	0.1093
S_hon	0.0998	0.0903	0.0883
S_bur	0.1076	0.1047	0.0996
S_lud	0.0936	0.0863	0.0848
S_opo	0.1128	0.0959	0.0971
S_til	0.1609	0.1528	0.1554
S_per	0.0889	0.0887	0.0820
S_koo	0.1010	0.0888	0.0952
S_mor	0.0986	0.0699	0.0756
S_mag	0.0768	0.0866	0.0796
S_bog	0.1385	0.1157	0.1231
S_ery	0.1305	0.1287	0.1222
S_ns3	0.0930	0.0819	0.0703
S_ang	0.0752	0.0693	0.0618
S_lui	0.0781	0.0753	0.0704
S_pau	0.0689	0.0665	0.0582
S_lil	0.0818	0.0753	0.0771
S_bak	[redacted]	0.0676	0.0613
S_parE	0.0303	[redacted]	0.0368
S_parW	0.0367	0.0118	[redacted]

Figure S1. Bayesian inferences that shows the phylogenetic relationships within *Sturnira* clade B, showing the posterior probabilities at each node: a) *cyt-b*, b) *D-loop*, c) *RAG1*. The height of enclosing triangles is proportional to the number of samples they contain. The colors indicate the following lineages: green--*S. parvidens* W, blue--*S. parvidens* E, and pink--*S. bakeri*.

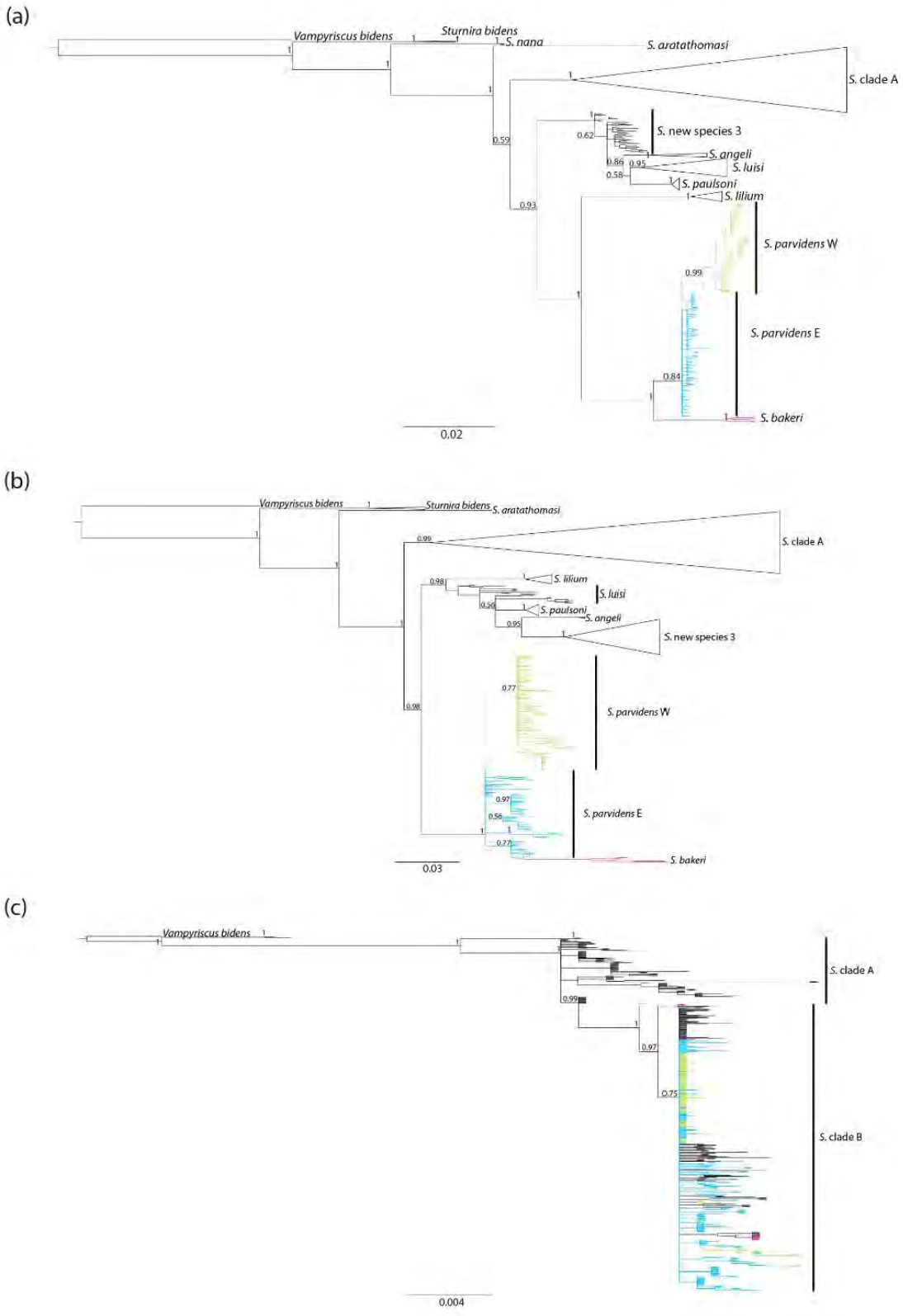

(a)
Vampyriscus bidens
Sturnira bidens
S. nana
S. aratathomasi
S. clade A
S. new species 3
S. angeli
S. luisi
S. paulsoni
S. lilium
S. parvidens W
S. parvidens E
S. bakeri
0.02
(b)
Vampyriscus bidens
Sturnira bidens
S. aratathomasi
S. clade A
S. lilium
S. luisi
S. paulsoni
S. angeli
S. new species 3
S. parvidens W
S. parvidens E
S. bakeri
0.03
(c)
Vampyriscus bidens
S. clade A
S. clade B
0.004

Figure S2. Mismatch distribution for *S. parvidens* (orange) and its haplogroups (green--*S. parvidens* West; blue--*S. parvidens* East), for each molecular marker (a, b, c: *cyt-b*; d, e, f: *D-loop*; g, h, i: *RAG1*). The colored lines indicate the frequency observed of pairwise differences, and the black line the frequency expected in a demographic model with population growth size.

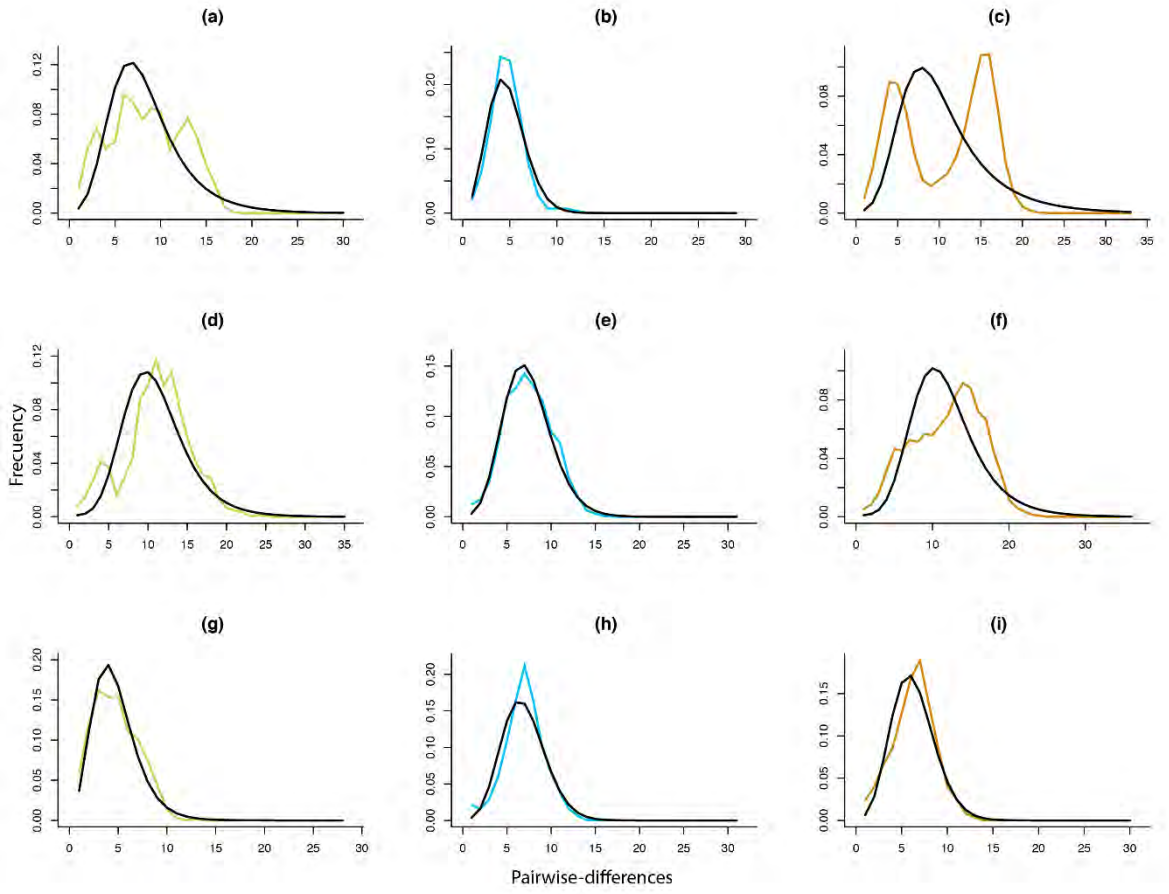


Figure S3. The contribution of the climatic variables on the two axes of the PCA and the percentage of inertia explained by the axes. Variables that characterize temperature were: annual mean (bio01_Ta), isothermality (bio03_Is), seasonality (bio04_Ts), maximum in the warmest month (bio05_Tw), and minimum in the coldest month (bio06_Tc); whereas variables that characterize precipitation were: total annual (bio12_Pa), total in wettest month (bio13_Pw), total in driest month (bio14_Pd), and seasonality (bio15_Ps).

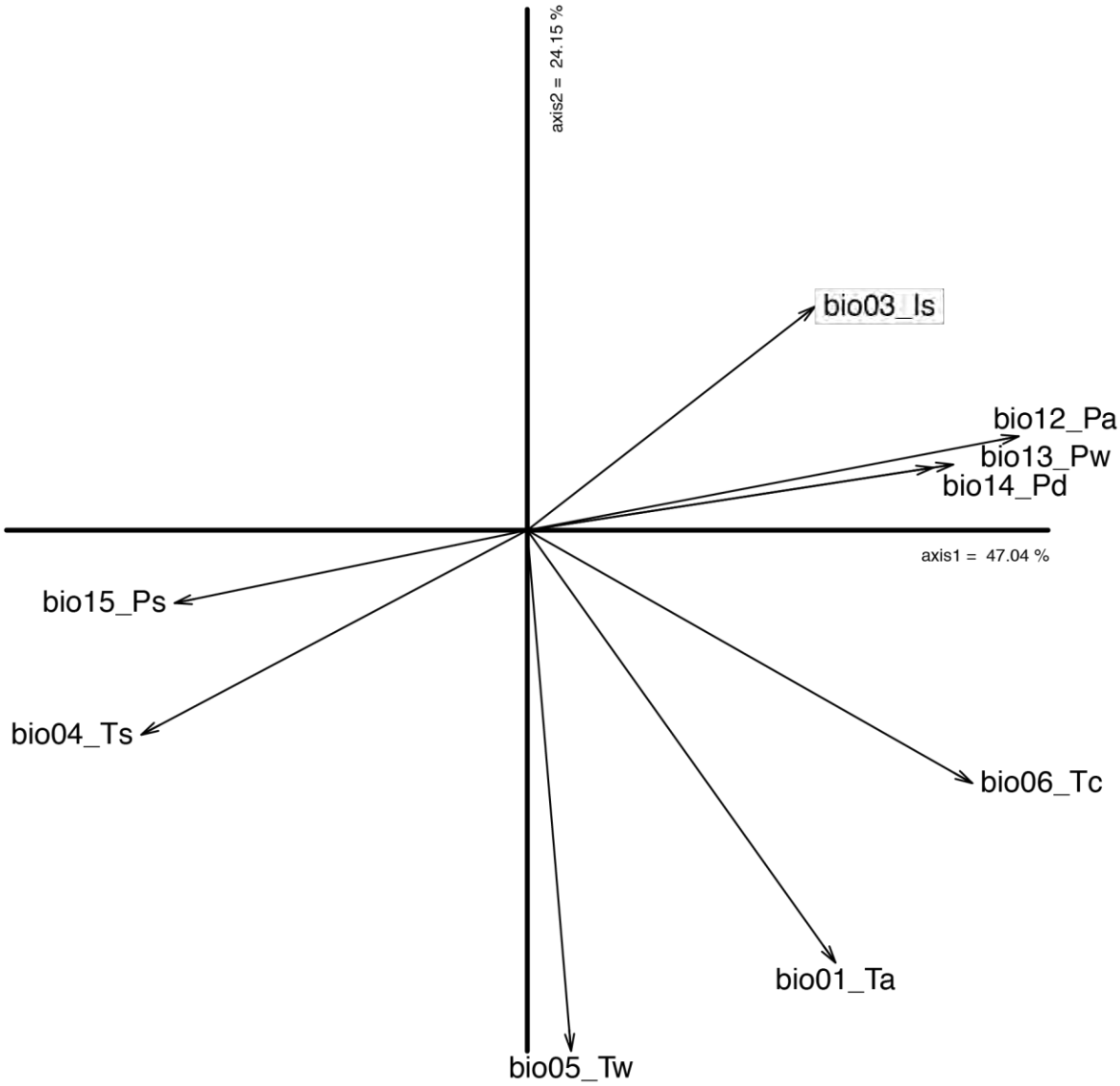
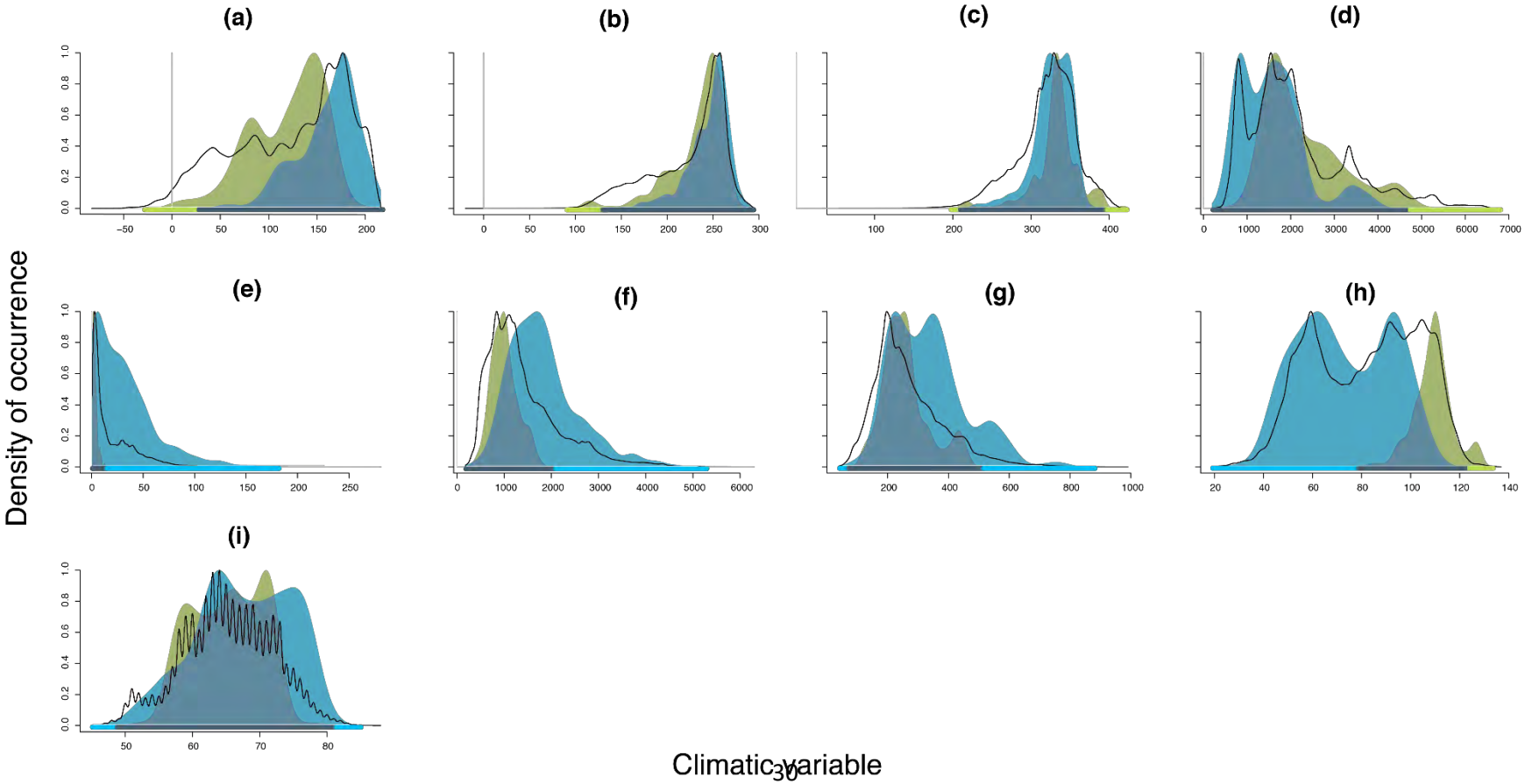


Figure S4. Niche overlap per climatic variable. The black line illustrates the available environment, and the green, blue and dark blue distributions represent the densities of occurrence of haplogroups West, East, and both, respectively. Variables that characterize temperature were: minimum in the coldest month (a), annual mean (b), maximum in the warmest month (c), seasonality (d), and isothermality (i); whereas variables that characterize precipitation were: total in driest month (e), total annual (f), total in wettest month (g), and seasonality (h)



CAPÍTULO 2.

Sturnira parvidens (Chiroptera: Phyllostomidae)

Manuscrito sometido: Mammalian Species (Fecha de envío: 26-febrero-2018)

Giovani Hernández-Canchola y Livia León-Paniagua

Resumen

El murciélago pequeño mesoamericano de hombros amarillos (*Sturnira parvidens* Goldman, 1917) es un murciélago de tamaño mediano, con un uropatagio vestigial, sin cola, y que usualmente presenta parches amarillentos o rojizos en los hombros. Habita en regiones tropicales asociadas a altitudes bajas y medianas, desde el norte de Costa Rica hasta México; y es una de las 21 especies validadas en el género *Sturnira*. A pesar de que principalmente se alimenta de plantas pioneras que son comunes en áreas perturbadas, *S. parvidens* utiliza refugios diurnos localizados en selvas maduras o en estados avanzados de sucesión. Actualmente no está incluido en ninguna categoría de riesgo y es considerado abundante. Sin embargo, la preservación de parches de selva madura dentro de paisajes modificados por el ser humano debe ser un importante eje rector para la conservación de esta especie.

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Sturnira parvidens (Chiroptera: Phyllostomidae)

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Keywords:	bat, frugivore, Little yellow-shouldered Mesoamerican bat, Mexico, Central America

MAMMALIAN SPECIES XX(XXXX):00-00

Sturnira parvidens (Chiroptera: Phyllostomidae)

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Abstract: The little yellow-shouldered Mesoamerican bat (*Sturnira parvidens* Goldman, 1917) is a medium-size yellow-shouldered bat with a vestigial uropatagium, no tail, and which usually has reddish or yellowish patches on the shoulders. It inhabits tropical habitats associated to lower and mid-elevations from northern Costa Rica to Mexico, and it is one of 21 validated species in the genus *Sturnira*. Although the species mainly feeds on pioneer plants that are common in disturbed areas, *S. parvidens* uses day roosts located in mature forest or in advanced successional stages. It is not currently in any threat category and is considered abundant. Nonetheless, the preservation of mature forest patches within human-dominated landscapes should be an important guiding principle for the conservation of this species. DOI: _____.

Key words: bat, frugivore, Little yellow-shouldered Mesoamerican bat, Mexico and Central America

Synonymy completed _____

Sturnira parvidens Goldman, 1917

Little yellow-shouldered Mesoamerican bat

Sturnira lilium: Dobson, 1878:540. Not *Sturnira lilium* É. Geoffroy Saint-Hilarie, 1810.

Sturnira lilium parvidens Goldman, 1917:116. Type locality "Papayo (about 25 miles northwest of Acapulco), Guerrero, Mexico."

Sturnira parvidens: Iudica, 2000:197. First use of current name combination.

CONTEXT AND CONTENT. Order Chiroptera, family Phyllostomidae, subfamily Stenodermatinae, tribe Sturnirini, genus *Sturnira*. This genus includes at least 21 recognized and validated species (Molinari et al. 2017): *Sturnira adrianae* Molinari et al., 2017; *Sturnira angeli* de la Torre, 1966; *Sturnira aratathomasi* Peterson and Tamsitt, 1968; *Sturnira bakeri* Velazco and Patterson, 2014; *Sturnira bidens* (Thomas, 1915); *Sturnira bogotensis* Shamel, 1927; *Sturnira burtonlimi* Velazco and Patterson, 2014; *Sturnira erythromos* (Tschudi 1844); *Sturnira hondurensis* Goodwin, 1940; *Sturnira koopmanhilli* McCarthy et al., 2006; *Sturnira lilium* (É. Geoffroy Saint-Hilaire, 1810); *Sturnira ludovici* Anthony, 1924; *Sturnira luisi* Davis, 1980; *Sturnira magna* de la Torre, 1966; *Sturnira mordax* (Goodwin, 1938); *Sturnira nana* Gardner and O'Neill, 1971; *Sturnira oporaphilum* (Tschudi 1844); *Sturnira parvidens* Goldman, 1917; *Sturnira paulsoni* de la Torre and Schwartz, 1966; *Sturnira perla* Jarrín-V and Kunz, 2011; and *Sturnira tildae* de la Torre, 1959. Nevertheless, there are two more species in the genus *Sturnira* that need to be characterized genetically to determine if they represent additional species, or are synonyms of recognized forms (Velazco and Patterson 2013): *Sturnira mistratensis* Contreras-Vega and Cadena, 2000; and *Sturnira sorianoi* Sánchez-Hernández et al., 2005. *Sturnira* new species 3 (*sensu* Velazco and Patterson 2013) also represents another genetic lineage, that needs to be characterized morphologically and described as a new species.

NOMENCLATURAL NOTES. *Sturnira parvidens* was considered as a subspecies of *S. lilium*. Nonetheless, it was concluded that *S. parvidens* should be recognized as species because of molecular evidence based on mitochondrial and nuclear molecular markers

(Iudica 2000; Velazco and Patterson 2013; Hernández-Canchola and León-Paniagua 2017). This conclusion is backed by morphological evidence (Goldman 1917; Iudica 2000; Sánchez-Hernández and Romero-Almaraz 2003). Nevertheless, before the radically subdivision of the *S. lilium* (*sensu lato*), all the reports about the biology and natural history of "*S. lilium*" were based on different species (e.g. *S. angeli*, *S. lilium*, *S. paulsoni*, *S. parvidens* and *S.* new species 3), so it is necessary to allocate existing information to the correct taxa (Velazco and Patterson 2014).

Sturnira comes from the latin *sturnirus* or *sturnus* (starling), possibly in memory of the "H. M. S. Starling", an escort vessel on which the type species of this genus was collected. The specific epithet *parvidens* comes from the latin *parvus* (little or small) and *dens* (teeth), that means "small teeth" (Gannon et al. 1989; Sánchez-Hernández et al. 2016).

DIAGNOSIS

Sturnira parvidens has four lower incisors whereas *S. bidens* and *S. nana* have only two functional inferior incisors (Molinari and Soriano 1987). Unlike most species of *Sturnira* (*S. adrianae*, *S. bogotensis*, *S. burtonlimi*, *S. erythromos*, *S. hondurensis*, *S. koopmanhilli*, *S. ludovici*, *S. magna*, *S. mordax*, *S. oporaphilum*, and the hypothetical *S. sorianoi*), in *S. parvidens* the entoconid and metaconid cusps are well defined and separated by a deep notch in m1-2 (Iudica 2000). The zygomatic arches are bowed outwards in *S. parvidens*, whereas they are straight in *S. bakeri* and *S. luisi* (Velazco and Patterson 2014). In *S. parvidens* the rostrum is longer than half of the braincase (Álvarez-Castañeda et al. 2015), whereas the rostrum is extremely blunt in *S. perla* (Jarrín-V and Kunz 2011). The skull in *S. parvidens* is shorter (greatest length of the skull, GLS = 21.2 mm [20.8—21.8]) than in *S. angeli* (GLS = 22.7 mm [22.4—23.1]), *S. bakeri* (GLS = 22.7 mm) and *S.*

paulsoni (GLS = 22.9 mm [22.1—23.5]—Jones and Phillips 1976; Velazco and Patterson 2014). *Sturnira parvidens* has a forearm smaller (36.2—42.5 mm) than *S. aratathomasi* (59—60.5 mm), *S. bakeri* (43—45 mm), *S. lilium* (40.2—46.2 mm), and *S. tildae* (45.01—48.42 mm—de la Torre 1961; Peterson and Tamsitt 1968; Jarrín-V and Kunz 2011; Velazco and Patterson 2014). The m1 in *S. parvidens* does not have a paraconulid cusp, a distinctive character in *S. mistratensis* (Contreras-Vega and Cadena 2000), of which a revaluation is needed (Velazco and Patterson 2013). Finally, there is no available information about the morphological characters that differentiate *S. parvidens* from *S.* new species 3 (*sensu* Velazco and Patterson 2013), except that the latest occurs in the Amazonia in South America (Velazco and Patterson 2014).

GENERAL CHARACTERS

Sturnira parvidens is a medium-size yellow-shouldered bat (Iudica 2000). The head is relatively short and broad, and the face is simple. The eyes are relatively large and the eyelids are endowed with eyelashes. The auditory pinnae are short, broad, rounded and pointed at the tips, with a simple long tragus and a large antitragus that forms a thickened horizontal ledge at the base of the ear. The noseleaf is small and broad, and its vertical portion is ovate-lanceolate. Two glandular ridges originate lateral to the anterior base of the noseleaf and continue dorsally until the level of the eyes. The nares are directed anteriorly and are located in the basal part of the noseleaf. The upper lip has small and variable warty growths. The lower lip has wart-like cutaneous pads: small pads forming a semicircular row surround a large central pad flanked by two others (Fig. 1—Dobson 1878; de la Torre 1961; Gannon et al. 1989).

The propatagium originates medially at the level of the shoulder. The plagiopatagium extends laterally down to the ankles and is sparsely haired with short hairs. The IV metacarpal is shorter than the III one. The species has a vestigial uropatagium, which is relatively sparsely haired with short hairs (4.0—5.00 mm); there is no tail and the calcaneus is short (de la Torre 1961; Velazco and Patterson 2014).

The fur is soft and dense, and is usually reddish or yellowish but it ranges from dark gray to dark red (Figs. 1 and 2). Juveniles are paler, and most individuals, especially adult males, have reddish or yellowish patches on the shoulders (Gannon et al. 1989; Téllez-Girón and Amin 2014). The dorsal pelage between the shoulders is bicolored and short (4.0—6.0 mm); ventrally the hairs are also short (4.0—6.0 mm) but tricolored. The proximal portion of the forearm is well furred with short hairs, the dorsal surfaces of the femur and tibia are sparsely covered with long hairs, and the dorsal surfaces of the feet are densely cover with long hairs (Velazco and Patterson 2014).

Ranges of typical measurements (mm or g) in 20 specimens from Belize (Bärtschi 2000; Fenton et al. 2000); 84 from Costa Rica, El Salvador, Mexico, Guatemala, Honduras and Nicaragua (de la Torre 1961; Velazco and Patterson 2014); 25 from Mexico: 15 from Chihuahua (López-González and García-Mendoza 2006), the female holotype in Guerrero (Sánchez-Hernández and Romero-Almaraz 2003), 9 in Oaxaca (Goodwin 1969); and 18 from Nicaragua (Genoways and Timm 2005) were: head and body length 57–70, hind foot length 12–15, ear length 15–17, forearm length 36.2–42.5 and weight 11.6–19.

Ranges of cranial measurements (mm) of 81 specimens from Costa Rica, El Salvador, Mexico, Guatemala, Honduras and Nicaragua (de la Torre 1961; Velazco and Patterson 2013); 25 from Mexico: 15 from Chihuahua (López-González and García-Mendoza 2006), the female holotype from Guerrero (Sánchez-Hernández and Romero-

Almaraz 2003), 9 from Oaxaca (Goodwin 1969); and 4 specimens from Nicaragua (Genoways and Timm 2005) were: greatest length of skull 20–23, condilobasal length 18.4–21.9, zygomatic breadth 12.1–13.9, mastoid breadth 10.8–12.1, breadth of braincase 9.5–10.2, interorbital width 5.2–7.1, maxillary toothrow length 5.8–6.9, and mandibular toothrow length 6.6–8.4 (Fig. 3).

DISTRIBUTION

Sturnira parvidens inhabits from Sonora in the Mexican Pacific Slope, and Tamaulipas in the Mexican Gulf Slope southward to Northern Costa Rica, including the Yucatan Peninsula (Fig. 4–Hernández-Canchola and León-Paniagua 2017). This bat can be found from 0 to 2000 m above sea level (Téllez-Girón and Amin 2014). There are two nearly allopatric genetic lineages inside the species, which are limited to the Sierra Madre del Sur (Michoacán, Guerrero and Oaxaca), on the Mexican Pacific Slope (Hernández-Canchola and León-Paniagua 2017).

FOSSIL RECORD

Sturnira parvidens has been recorded from Late Pleistocene material (Rancholabrean) from Loltún Grotto, on the Yucatan Peninsula of Mexico (Arroyo-Cabrales and Polaco 2008). There are further records from the Late Pleistocene or Holocene from Cebada Cave, Chiquibil System in Belize (Fig. 4–Czaplewski et al. 2003).

FORM AND FUNCTION

Form.—The rostrum of *Sturnira parvidens* is broad, the basisphenoid pits are shallow and divided by a high septum, the sphenorbital fissure is oval, the anterior process of the glenoid fossa is well developed, and the proximal end of the stylohyoid is expanded (Velazco and Patterson 2014). The maxillary toothrow is U-shaped and slightly convergent. The palatal fossa is U-shaped, with divergent tips (Sánchez-Hernández and Romero-Almaraz 2003). The dental formula is i 2/2, c 1/1, p 2/2, m 3/3, total 32. The upper incisors are bilobed and the external lobule is smaller (Sánchez-Hernández and Romero-Almaraz 2003). M3 have two labial cusps (Velazco and Patterson 2014). The lower incisors are trilobed, nevertheless these teeth wear down with age as in other member of the genus *Sturnira* (Hershkovitz 1949; Sánchez-Hernández and Romero-Almaraz 2003). The lower canines are laterally divergent shafted outward (Velazco and Patterson 2014). The entoconid and metoconid are well defined and separated by a deep notch in m1—2, and these lingual cusps are square (Sánchez-Hernández and Romero-Almaraz 2003).

The brain of *S. parvidens* closely resembles the one of *S. hondurensis*. It has deep and extremely smooth cerebral hemispheres. The pseudocentral sulci and sulci anterior to the pseudocentral sulci are poorly developed compared with other stenodermatine bats. The pseudotemporal lobes are angular and project ventrally. The inferior colliculi are completely covered, and the cerebellums is simple and with a medial crest (McDaniel 1973).

The stomach of *S. parvidens* is also similar, but less robust, to the one of *S. hondurensis*. This is simple with a well-developed, elongate and tapered cardiac vestibule. The cardiac caecum is small, and the fundic caecum is saccular and thin-walled, which forms a spacious chamber with an apex. The pyloric tube is long and narrow, and the

pyloric valve is vestigial. The gastroesophageal junction lies well superior to the gastroduodenal junction, and the latter is clearly marked. The corpovestibular and vestibulocaecal junctions are marked by distinct sulci that anastomose near the midregion of the stomach. The tunica muscularis is bilaminate and the tunica submucosa forms the rugae, which in general are longitudinally oriented; there are numerous branches forming transverse secondary folds, but the elastic fibers are not many. In the tunica mucosa, cardiac glands surround the gastroesophageal junction, and they are weakly reactive or non reactive to demonstrate the presence of acid mucopolysaccharides. Oxyntic glands occupy the cardiac vestibule, the cardiac caecum and a portion of the corpus. In the basal third of these glands, there are numerous alpha chief cells and few mucous gland cells. As oxyntic glands disappear, transitional glands (mainly mucous cell glands) become increasingly more apparent. There are cells within the bases of the pyloric glands, which are histologically identical to the submucosal glands of Brunner located in the uppermost duodenum (Rouk 1973; Forman et al. 1979). In three specimens from Mexico, the gut mass was 1.19 g ± 0.17 SD, and the gut area 9.58 cm^2 ± 0.12 SD (Schondube et al. 2001). In four adult bats from Jalisco (Mexico), an intestinal area of 18.9 cm^2 ± 1.5 SD and an intestinal length of 27.7 cm ± 1.3 SD was measured by Hernández and Martínez del Río (1992).

In Oaxaca, the wing aspect ratio of this species was 6.03, and the relative wing loading was 11.98 (García-García et al. 2014). The hair of *S. parvidens* does not have a medulla, and the scales are coronal and unequal hastate (Baca-Ibarra and Sánchez-Cordero 2004).

Function.—In four adult *Sturnira parvidens* from Jalisco, the average disaccharidase activity was measured as (µmol/min*cm^2 ± SD): maltase = 5.5 ± 1.1,

sucrase = 1.6 ± 0.3, isomaltase = 0.3 ± 0.1, and there was no evidence of trehalase and lactasae activity. The apparent binding constant for sucrase was 56.8 ± 4.7 mM (Hernández and Martínez del Río 1992). In three other bats, the values obtained for the intestinal enzymes were: total activity (μmol/min ± SD): maltase = 22.36 ± 11.92, sucrase = 7.51 ± 4.87, Aminopeptidase-N = 3.12 ± 0.319, trehalase = trace; pH optima: maltase = 6, sucrase = 5.5, Aminopeptidase-N = 7, trehalase = 6.5; K_m (binding constant): maltase = 12.10, sucrase = 48.48, Aminopeptidase-N = 2.37; total V_{max} (maximal hydrolysis rate): maltase = 32.04, sucrase = 20.51, Aminopeptidase-N = 3.39 (Schondube et al. 2001). These results are congruent with the diet consumed by *S. parvidens*, whereas maltose, sucrose and isomaltose are commonly present in plant parts and trehalose is rare in plants, but common as storage sugar in insects (Hernández and Martínez del Río 1992). For seven specimens, the coefficients of apparent assimilation of sugar solutions were glucose = 0.97 ± 0.01 SD, fructose = 0.94 ± 0.02 SD and sucrose = 0.93 ± 0.03 SD. Despite this, *S. parvidens* preferred solutions dominated by sucrose over glucose and fructose (Herrera 1999), and there was a negative exponential relationship between intake volume and sugar concentration (Saldaña-Vázquez et al. 2015). In Veracruz (Mexico) the digestive capacity calculated for *S. parvidens* was 0.65 and its Shannon index of diet diversity was 3.9 (Saldaña-Vázquez et al. 2015), whereas in Costa Rica the niche breadth was 0.91 (Heithaus et al. 1975). The high digestive capacity could be related to the ability to ingest low and high quality food, including fruits avoided by *S. hondurensis*, a congener with a lower diet diversity that in some places is sympatric with *S. parvidens* (Saldaña-Vázquez et al. 2015).

In Jalisco, the calculated urine concentration (mOsmol/kg H_2O) for one specimen during the dry season was 874, whereas in the rainy season it was 342.5. The percentage of

fecal water content in two specimens collected during the dry season was 64.1% ± 8.1 SE (Pilosof and Herrera 2010). The δ^{15} (stable isotope ratio of nitrogen – ^{15}N:^{14}N) in 3 bats from Mexico was 3.81 (SD = 0.62), a similar value to other frugivorous bats (Schondube et al. 2001). In captivity, hypothermia is a thermoregulatory strategy that allows to *S. parvidens* to adjust its metabolic rate to feeding success and the level of fat stores, because the body temperature was highly correlated with body mass and not with time in captivity (Audet and Thomas 1997).

In Honduras, the stable hydrogen isotope ratio ($^2H/^1H$ or δD) in hair keratin was -93.3 % (± 12.3 SD) at 1,202 meter above sea level (Erzberger et al. 2011). In Nicaragua, the δD in claw keratin was -67.6 % (± 11.6 SD) and -64.6 % ± (± 3.5 SD) in hair keratin (Fraser et al. 2010). In Tabasco (Mexico), one of 228 individuals showed signs of alopecia, possibly because of anthropogenic activities (Bello-Gutiérrez et al. 2010). Finally, a reproductive male from Oaxaca showed signs of partial albinism, with white spots on the tips of both wings and discolored hairs in the ventral sides of the body (Zalapa et al. 2016).

ONTOGENY AND REPRODUCTION

The female reproductive tract consists of two functional ovaries, two oviducts and a simple uterus. Although there is evidence that the right ovary is heavier, larger and more irrigated than the left, follicles at different stages of development and the same number of oocytes have been detected in both ovaries (Antonio-Rubio et al. 2013; Álvarez-Guerrero et al. 2014). Females of *Sturnira parvidens* have polarized ovaries, and cells located in the cortical region are surrounded by flat spindle cells that comprise the primordial follicles. In

these, adult cortical germ cell groups may represent progenitor cells of the germline involved in maintaining the renewal of oocytes and follicles in adult ovaries (Antonio-Rubio et al. 2013).

The sperm of *S. parvidens* consists of a head (mean = 7.01 μm) and a tail, which is divided in the mid-piece (mean = 20.33 μm), the main piece and the end piece (mean = 70.50 μm). The shape of the head is oval and/or elongated, and the acrosome is clearly visible using light microscopy. The tail is inserted in the center of the head, but there are a small percentage of sperm with lateral insertion. The sperm calculated concentration is 5.15 x 10^6 sperm per mL, with a viability of 83.82 %, and a motility of 60 % at 37° C. 70.53 % of the sperm has normal appearance, and the more frequent abnormalities detected were different arrangement of coiled tail, a small proportion of folded mid-pieces, defects in the mid-piece mainly characterized by the presence of cytoplasmic droplets at different points, and dispersed tails and heads (Álvarez-Guerrero et al. 2014).

Young specimens of *S. parvidens* have been collected during January (Mexico: Jalisco), March (Nicaragua), May (Mexico: Guerrero), June-August (Mexico: Jalisco), October (Mexico: Colima—Genoways and Timm 2005; Iñíguez-Dávalos 2005; Almazán-Catalán et al. 2015; Sánchez-Hernández et al. 2016). Whereas subadults were collected during January, June-August, October-November (Mexico: Colima—Sánchez-Hernández et al. 2016).

Males with scrotal testes were collected in January (Mexico: Colima), March (Mexico: Guerrero), April-May (Belize; Mexico: Jalisco), June (Mexico: Jalisco), August (Mexico: Jalisco), October-November (Mexico: Jalisco—Watkins et al. 1972; Bärtschi

2000; Iñíguez-Dávalos 2005; Sánchez-Hernández et al. 2009, 2016; Almazán-Catalán et al. 2015).

It seems that *S. parvidens* usually has one embryo per pregnancy (Cockrum and Bradshaw 1963; Briones-Salas 2000; Sánchez-Hernández et al. 2009). Pregnant females were found during January (Costa Rica; Mexico: Campeche, Colima, Jalisco and Querétaro), February (Costa Rica; Guatemala; Mexico: Jalisco and Veracruz), March (Guatemala; Mexico: Jalisco and Veracruz), April (Mexico: Colima, Jalisco, Oaxaca, Quintana Roo, Sinaloa and Veracruz), May (Costa Rica; Guatemala; Mexico: Sinaloa and Veracruz), June (Costa Rica; Guatemala; Mexico: Jalisco, Sinaloa, Veracruz and Zacatecas), July (Guatemala; Mexico: Campeche, Durango, Jalisco and Veracruz; Nicaragua), August (Guatemala; Mexico: Sinaloa, Quintana Roo and Veracruz), September (Mexico: Jalisco, Sonora and Veracruz), October (Mexico: Jalisco and Veracruz), November (Mexico: Veracruz), and December (Costa Rica—Genoways and Jones 1968; Wilson 1979; Estrada and Coates-Estrada 2001; Iñiguez-Dávalos 2005; Sánchez-Hernández et al. 2009, 2016).

There are two axillary mammary glands (de la Torre 1961), and females with prominent tits were collected during April (Mexico: Jalisco) and June-October (Mexico: Jalisco—Watkins et al. 1972). Lactating females were found during January (Costa Rica; Belize; Mexico: Colima and Veracruz), February-March (Costa Rica; Mexico: Veracruz), April (Costa Rica; Mexico: Colima, Jalisco, Veracruz), May (Costa Rica; Guatemala; Mexico: Chiapas, Colima, Jalisco, and Veracruz), June (Mexico: Chiapas, Durango, Guerrero, Jalisco, Sinaloa and Veracruz), July (Costa Rica; El Salvador; Mexico: Colima, Durango, Jalisco and Veracruz; Nicaragua), August (Costa Rica; Mexico: Colima, Jalisco

and Veracruz), September (Mexico: Colima, Jalisco and Veracruz), October (Mexico: Jalisco and Veracruz), November (Mexico: Colima and Veracruz) and December (Mexico: Oaxaca and Veracruz—Jones 1963; Wilson 1979; Fenton et al. 2000; Estrada and Coates-Estrada 2001; Iñiguez-Dávalos 2005; Almazán-Catalán et al. 2015; Sánchez-Hernández et al. 2016). In Jalisco, the lactating period was found to relate with the peak of fruiting of *Solanum nigricans*, a plant consumed by *Sturnira parvidens* (Iñiguez-Dávalos 2005).

The reproductive pattern of *S. parvidens* in a tropical rain forest (Veracruz) where there is little seasonality in food availability was interpreted as a seasonal polyoestry (Estrada and Coates-Estrada 2001). In a tropical dry forest from Costa Rica, *S. parvidens* reproduces twice each year, once during dry season and once with the fruit abundance in the wet season (Humphrey and Bonaccorso 1979). Sánchez-Hernández et al. (1986) reviewed and analyzed the reproductive pattern of *S. parvidens* in the tropical deciduous forest of the Mexican Pacific Slope (from Nayarit to Oaxaca). They concluded that the species has three peak pregnancy periods (February—March, July—September, and November—December), two lactation periods (April—June and September—November), and three periods where juveniles were captured (February—March, May—June, and October—November), suggesting a continuous polyestrous reproductive pattern with three periods of maximal reproductive pattern, in a region with a strong seasonality.

ECOLOGY

Space use.—*Sturnira parvidens* mainly inhabits tropical habitats associated with lower and mid elevations (Villalobos and Valerio 2002; Téllez-Girón and Amin 2014). It

has been captured in the understory or in the subcanopy of tropical, subtropical, deciduous, riparian and secondary forests and ecotones, but also in xeric scrubs and temperate and cloud forests (Briones-Salas 2000; Vargas-Contreras and Hernández-Huerta 2001; Iñiguez-Dávalos 2005; Vargas-Miranda et al. 2008; Estrella et al. 2014; López-González et al. 2014; Briones-Salas et al. 2016; Zarazúa-Carbajal et al. 2017). This species is commonly encountered over watercourses and bodies of water, fruit crops or agricultural fields, across roads, trails or margins of the forest, and in canyons or archeological sites (Cockrum and Bradshaw 1963; Jones 1963; Baker et al. 1967; Watkins et al. 1972; Fenton et al. 2000; Álvarez-Castañeda et al. 2008; Estrella et al. 2014; Almazán-Catalán et al. 2015).

Sturnira parvidens is considered as an indicator of forest disturbance (Schulze et al. 2000), because in many places it is more abundant in the early stages of secondary succession than in old secondary and tropical evergreen forests (García-Morales et al. 2014). Nevertheless, this assumption must be carefully interpreted. For example: in Chiapas (Mexico), *S. parvidens* was more abundant in secondary forests managed with the pioneer balsa tree (*Ochroma pyramidale*) than in secondary forests without management and in mature rain forests. Actually, mature forests and without management forests show similar abundances of *S. parvidens* (Vleut et al. 2013). In addition, in the Mexican state of Veracruz the abundance of *S. parvidens* was higher in cloud forest fragments than in coffee plantations, due to the lower density of chiropterochorous plants available in the coffee fields (Saldaña-Vázquez et al. 2010). In state of Veracruz *S. parvidens* was the most abundant species in a small evergreen rainforest surrounded by anthropogenic landscape (Ramírez-Lucho et al. 2017). Although the species is not very sensitive to fragmentations (García-García et al. 2014), there is an inversely proportional relationship between

abundance of the species and distance to primary forest edge, suggesting that *S. parvidens* forages in secondary forest but for other activities needs to be close to primary forests (Castro-Luna et al. 2007; García-Morales et al. 2014).

It was believed that *S. parvidens* uses day roosts in caves, culverts or buildings, due to high levels of infestation by bat flies, with other no direct reports. However, the captures in mist nets indicate that the species could use caves only as night roosts (Fenton et al. 2000; Cuxim-Koyoc et al. 2015). Actually, during 7 months of sampling in Chiapas, only four specimens were collected 15 meters away to the entrance of a cave, suggesting that is difficult to find this species inside caves (Tlapaya-Romero et al. 2015).

Sturnira parvidens mainly uses day roosts in standing tree cavities, which are inconspicuous, difficult to flush and easily overlooked. It prefers to roost close to the entrances, mainly in trees with only one cavity located from 2.0 to 8.2 m above the ground, where there are lower levels of moisture (81.93 ± 6.45 %, minimal = 76.00 ± 6.30 %, maximum = 86.40 ± 5.88 %) than those in the exterior (89.07 ± 5.48 %, minimal = 78.33 ± 8.65 %, maximum = 92.40 ± 4.47 %). Those trees usually have a lot of foliage, a diameter at breast height from 26.1 cm to 3.3 m, and they are generally higher and larger in diameter than the other ones in the periphery in places with closed vegetation. These features are rare inside habitat of *S. parvidens*, and mainly are found in places of mature forest or in advanced successional stages (Wohlgenant 1994; Fenton et al. 2000; Evelyn and Stiles 2003; Ortiz-Ramírez et al. 2006). In Lamanai (Belize—Fenton et al. 2000), Campeche (Evelyn and Stiles 2003), and Chiapas (Ortiz-Ramírez et al. 2006) cracks, branch and woodpecker holes, or holes were recorded as roosts. These roots were located in the following plant species: *Brosimum alicastrum*, *Bucida buceras*, *Bursera simaruba*,

Guazuma ulmifolia, *Manilkara zapota*, *Metopium brownei*, *Pimenta dioica*, *Pimenta officinalis*, *Pithecellobium arboretum*, *Pouteria reticulata*, *Pseudobombax ellipticum*, *Sideroxylon salicifolium*, *Talisia floresii* and *Vitex gaumeri* (Fenton et al. 2000; Evelyn and Stiles 2003; Ortiz-Ramírez et al. 2006). The species also roots in small gaps in vine tangles such as *Distictis* spp., *Solanum* spp., or in the bases of palm fronds like *Attalea cohune* (Fenton et al. 2000). Additionally, some bats were found in a riverbank hole (Evelyn and Stiles 2003), and a small colony in a termite nest on a tree, approximately 2.5 m above the ground (Sánchez-Hernández et al. 2016).

Costa Rican specimens of *S. parvidens* showed activity patterns throughout the night, with the highest peak of activity at the beginning of the night (Brown 1968). In Tamaulipas, there is a high temporal overlap (not statistically significant) during foraging with its congeneric *S. hondurensis* (Arriaga-Flores et al. 2012), and in Costa Rica *S. parvidens* was found to forages singly (Heithaus et al. 1975). Radio-tagged bats usually roosted alone and emerged later than bats without radio tags. In Belize, the longest distance traveled by *S. parvidens* was 3.2 Km, but most bats have been captured between 50-1400 m (mean = 636 ± 511 m; n = 9) from their roosts (Fenton et al. 2000). During a census over two years in Veracruz, from 367 captures 14 individuals were recaptured at a mean distance of 2246 m (from 500 to 6500 m) of distance of the original place of capture (Estrada et al. 1993). In the same Mexican state but during one year of census, seven of 263 *S. parvidens* were recaptured after 1 to 153 days, at a mean distance of 348 m (from 0 to 692 m—Galindo-González and Sosa 2003). 18 of 100 Costa Rican *S. parvidens* were recaptured at a mean distance of 270. 2 m, and some of them were recaptured 2 to 3 years after banding

(Fleming et al. 1972). Other 38 from 182 bats in Costa Rica were recaptures at a mean distance of 424.3 m (Heithaus et al. 1975).

In the state of San Luis Potosí, Mexico, *S. parvidens* was more abundant during the rainy season than during the dry season, possibly by the moving out the area as a result of seasonal changes in resource availability (García-Morales et al. 2014). The opposite pattern occurred in Costa Rica (Heithaus et al. 1975). In Nicaragua, more negative values of δD keratin than predicted in the capture site, possibly indicate that tissue synthesis was at higher elevation followed by migration downslope to the capture site (Fraser et al. 2010). Whereas sex proportion is similar in sub-adults, adult females are more frequently found than adult males (Iudica 2000; Estrada and Coates-Estrada 2001; Iñiguez-Dávalos 2005).

In Michoacán, the ecological characterization of *S. parvidens* shows that the species inhabits tropical deciduous forest with temperatures of 8—32° C and levels of precipitation of 800—1500 mm (Wang et al. 2003). Otherwise, the two haplogroups found in the species (Hernández-Canchola and León-Paniagua 2017) show signals of an upward climatic niche differentiation over time, at least since the Last Interglacial. The populations located in Western Mexico are able to inhabit in more extreme temperatures, particularly cooler temperatures during the coldest month, and places with more seasonality in temperature and precipitation. This environmental differentiation apparently decreases the probability of admixture of genetic lineages (Hernández-Canchola and León-Paniagua 2017).

Diet.—*Sturnira parvidens* has been reported as a good seed disperser, for example in pastures which were rainforests (Galindo-González et al. 2000), coffee plantations (García-Estrada et al. 2012) and rainforest (Lou and Yurrita 2005; García-Morales et al.

2012). Over the course of a night, the species is able to visit habitats in different stages of regeneration, exchanging seeds between disturbed and mature forests, and creating plant connections between fragmented and continuous landscapes (Galindo-González et al. 2000; García-Estrada et al. 2012; García-Morales et al. 2012; Bolívar-Cimé et al. 2014).

Sturnira parvidens primarily feeds on the fruit of plants of early vegetation succession, mainly the fruits of pioneer herbs, pioneer shrubs and some pioneer trees (Olea-Wagner et al. 2007; García-Morales et al. 2012; Kraker-Castañeda et al. 2016). The species prefers *Piper* and *Solanum* fruits (Lou and Yurrita 2005); nevertheless, there is a geographically dietary shift. In some places there is an overlapping food niche with the bats genus *Carollia*, whereas in others there is none (Heithaus et al. 1975; Lou and Yurrita 2005; Kraker-Castañeda et al. 2016). In Costa Rica, the fruits recorded as its diet are *Cecropia* spp., *Chlorophora tinctora*, *Muntingia calabura*, *Piper tuberculatum*, *Solanum hirtum* and *Solanum* spp. (Heithaus et al. 1975). In Chiapas, *Ageratum* spp., *Capsicum annuum*, *Cecropia obtusifolia*, *Cecropia peltata*, *Drymaria* spp., *Juanulloa mexicana*, *Miconia mexicana*, *Peperomia* spp., *Piper auritum, Piper hispidum*, *Piper lapathifolium*, *Piper pseudolindenii*, *Piper* spp., *Salvia* spp., *Saurauia kegeliana*, *Saurauia madrensis*, *Solanum americanum*, *Solanum chrysotrichum*, *Solanum diphyllum*, *Solanum ochraceo-ferrugineum*, *Solanum torvun* and *Trophis chiapensis* (Olea-Wagner et al. 2007; García-Estrada et al. 2012). In Hidalgo (Mexico) *Cecropia obtusifolia*, *Coussapoa purpusii*, *Ficus* sps., *Markea* spp., *Physalis* spp., *Piper amalago*, *Piper hispidum*, *Solanum diphyllum*, *Solanum rudepanum* and *Trema micrantha* (García-Morales et al. 2012). In Jalisco *Solanum aphyodendrin*, *Solanum appendiculatum* and *Solanum nigricans* (Iñiguez-Dávalos 2005). In Puebla (Mexico) *Ficus obtusifolia*, *Ficus* spp., *Manilkara zapota*, *Myrtillocactus*

geometrizans and *Sideroxylon palmeri* (Herrera et al. 2013; Herrera and López 2017). In San Luis Potosí *Ficus cotinifolia*, *Maclura tinctoria*, *Piper hispidum*, *Piper* spp., *Piper yzabalanum*, *Solanum diphyllum* and *Solanum erianthun* (García-Morales et al. 2012). In Yucatán (Mexico) *Ficus cotinifolia*, *Ficus* spp., *Maclura tinctoria* and *Solanum erianthum* (Bolívar-Cimé et al. 2014). In Veracruz *Hedyosmum mexicanum*, *Lycianthes geminifolia*, *Piper hispidum*, *Piper lapathifolium*, *Solanum aphyodendron*, *Solanum schlechtendalianum* and *Vismia mexicana* (Hernández-Montero et al. 2015). In Northern Guatemala *Cecropia obtusifolia*, *Cecropia peltata*, *Ficus padifolia*, *Ficus* spp., *Piper aduncum*, *Piper aeruginosibaccum*, *Piper amalago*, *Piper auritum*, *Piper scabrum*, *Solanum schlechtendalianum*, *Solanum torvum*, *Solanum umbellatum*, *Vismia camparaguey* (Kraker-Castañeda et al. 2016). In Petén (Guatemala) *Cecropia obtusifolia*, Moraceae spp., *Piper aeruginosibaccum*, *Piper amalago*, *Piper auritum*, *Piper martensianum*, *Piper psilorachis*, *Piper sempervirens*, *Solanum brodgettii*, *Solanum erianthum*, *Solanum nudum* and *Solanum torvum* (Lou and Yurrita 2005). Further, in Costa Rica some specimens carried pollen of the following plants: *Anacardium excelsum*, *Bauhinia pauletia*, *Bauhinia ungulata*, *Bombacopsis fendleri*, *Ceiba aesculifolia*, *Ceiba pentandra*, *Crescentia* spp., *Hymenaea courbaril*, *Mangifera indica*, *Manilkara zapota*, *Ochroma lagopus*, *Pseudobombax septinatum* (Heithaus et al. 1975), and in Puebla *Sturnira parvidens* carried pollen of *Pachycereus weberi* and *Pilosocereus chrysacanrhus* (Valiente-Banuet et al. 1997). To nurse the young, the Costa Rican *S. parvidens* changes its diet from frugivory in the wet season to nectarivory in the dry season (Heithaus et al. 1975; Humphrey and Bonaccorso 1979). There is evidence that the species also consumes flowers of plants in the piper family (Sánchez-Hernández et al. 2016), and some insects in the Order Hymenopthera and

Diptera (Herrera and López 2017). In experimental conditions, *S. parvidens* prefers to eat fruits of *Conostegia volcanalis* over *Solanum aphyodendron* (Iñiguez-Dávalos 2005).

Diseases and parasites.—*Sturnira parvidens* is highly ectoparasitized by the bat flies (Diptera: Streblidae) *Aspidoptera delatorrei*, *Aspidoptera falcata*, *Megistopoda proxima* (Dick 2013; Cuxim-Koyoc et al. 2015), and potentially a new species of the genus *Trichobius* (Ramírez-Martínez et al. 2016). The presence of the bat flies *Metelasmus pseudopterus*, *Nycterophilia coxata* and *Trichobius intermedius* in *S. parvidens* are considered accidental or contamination transfers (Dick 2006, 2013).

Mites found on *S. parvidens* are: *Chirnyssoides brasiliensis*, *Eudusbabekia lepidoseta*, *Eudusbabekia viguerasi*, *Paralabidocarpus tonatiae*, *Parichoronyssus euthysternum*, *Periglischrus ojastii*, *Periglischrus vargasi*, *Steptolaelaps liomydis* (Colín-Martínez and García-Estrada 2016; Ramírez-Martínez et al. 2016; Colín-Martínez et al. 2018), in addition to the ones reported by Webb and Loomis (1977): *Hooperella vesperuginis*, *Microtrombiula sturnirae*, *Paralabidocarpus artibei*, and *Periglischrus iheringi*.

In Morelos (Mexico—Villegas-García and Santillán-Alarcón 2004) and in Yucatan Peninsula (López-Cancino et al. 2015) it has been reported that *Sturnira parvidens* is a host of *Trypanosoma cruzi*. In Chiapas, Tabasco, and Jalisco *S. parvidens* is a host of *Leishmania* (L.) *mexicana* (Berzunza-Cruz et al. 2015). In Guatemala, the presence of the bacteria *Bartonella* spp. was confirmed in one of twelve specimens of *S. parvidens* (Bai et al. 2011).

No evidence of dengue virus (types 1—4) were detected in Guatemala (Sotomayor-Bonilla et al. 2014) and Yucatán (Machain-Williams et al. 2013). Nevertheless, in Veracruz one of 14 bats was positive for dengue virus NS-1 protein (Aguilar-Setién et al. 2008). In Mexican areas with concurrent dengue cases, *S. parvidens* and other bats are not involved as reservoirs in dengue virus sylvatic cycle (Cabrera-Romo et al. 2016).

Three of 63 *S. parvidens* from Guatemala were hosts of a divergent influenza A virus (subtype "H17"—Tong et al. 2012). 37.8 % of 37 *S. parvidens* collected in Colima were positive for antirabic antibodies, 12 of them were collected in undisturbed places and two in disturbed areas. In the same bats, there were no evidence of the La Piedad Michoacan virus (genus *Rubulavirus*), which causes the blue eye disease (Salas-Rojas et al. 2004). There was also no evidence of Coronaviruses in Campeche (6 bats from undisturbed and 6 from disturbed areas), and in Chiapas (22 specimens from a disturbed area—Anthony et al. 2013).

In 54 *S. parvidens* sampled in Guatemala, 2 bats were positive to the Venezuelan equine encephalitis virus (TC83 strain, variant I-A/B), 4 bats to the vesicular stomatitis virus (VS New Jersey Greentree strain), 4 bats to the Eastern equine encephalitis virus (NJ-160 strain), and 12 bats to the Rio Bravo virus (M64 strain). Four of 53 bats were positive to the St. Louis encephalitis virus (MSI-7 strain). There was no evidence of vesicular stomatitis virus (VS-Indiana laboratory strain), Venezuelan equine encephalitis virus (Mena II strain, variant I-E), Western equine encephalitis (Fleming MI-29559B strain), Tacaribe virus (11573 strain), and Nepuyo virus (P55MI strain—Ubico and McLean 1995). In six bats from Chiapas and 6 from Campeche, one in Chiapas was positive to Venezuelan equine encephalitis virus subtype IAB, and none were positive for eastern equine

encephalitis virus, western equine encephalitis virus, and West Nile virus (Sotomayor-Bonilla et al. 2017). In nine bats from Yucatán, there was no evidence of antibody prevalence of the West Nile virus or the St. Louis encephalitis virus (Machain-Williams et al. 2013).

Interspecific interactions.—*Sturnira parvidens* could *co-occur* with other *Sturnira* species such as *S. hondurensis* and *S. luisi*, and commonly is collected with other frugivorous or nectarivorous bats. *Sturnira parvidens* has been collected with many other bats, such as species in the genus *Artibeus*, *Carollia*, *Centurio*, *Chiroderma*, *Desmodus*, *Diphylla*, *Eptesicus*, *Eumops*, *Glossophaga*, *Idionycteris*, *Lasiurus*, *Leptonycteris*, *Molossus*, *Myotis*, *Noctilio*, *Platyrrhinus*, *Pteronotus*, *Rhogeessa*, *Tadarida* and *Uroderma* (Jones 1964; Watkins et al. 1972; Urbano-Vidales et al. 1987; Genoways and Timm 2005). It has been reported that it roosts with other species of bats such as *Carollia perspicillata*, *Choeroniscus godmani* and *Saccopteryx bilineata* (Ortiz-Ramírez et al. 2006), but in captive and experimental conditions *Sturnira parvidens* avoided roosting with *Desmodus rotundus* (Wohlgenant 1994).

BEHAVIOUR

In captivity, some *Sturnira parvidens* roosted together (Wohlgenant 1994), but in the wild the species tends to roost mainly alone or in small groups (most of the times 1—3 bats, or in few cases 4, 5, 10, or more bats—Fenton et al. 2000). Roosts of males and females are indistinguishable, and a lactating female was found roosting in a hollow tree. A sub-adult female of *S. parvidens* changed its roost at least 3 times in 14 days, nevertheless,

adults of this species are considered as a roost-faithful (Fenton et al. 2000; Evelyn and Stiles 2003).

GENETICS

The karyotype of *Sturnira parvidens* (2n = 30, FN = 56) is identical to the one in *S. hondurensis* (Baker 1967; Hsu et al. 1968), and possibly identical to other species in the genus *Sturnira* (Gannon et al. 1989). The X chromosome is fairly large and subtelocentric and the Y chromosome is small and submetacentric. Its autosomal chromosomes (in pairs) are: 7 metacentrics, 3 submetacentrics and 4 subtelocentrics (Baker 1967). Through fluorescent in situ hybridization, Baker et al. (1992) detected that only two medium subtelocentric chromosomes possess ribosomal genes (rDNA).

Sequences of the mitochondrial cytochrome b and cytochrome c oxidase subunit 1 (COI) were used to analyze the geographically and genetically distinct groups within *S. lilium* (*sensu lato*). These research suggested that Mesoamerican samples, previously identified as *S. lilium*, could represent a distinct and independent lineage (Ditchfield 2000; Hajibabaei et al. 2007; Clare et al. 2011). Nevertheless, the review of genus *Sturnira* based on partial cytochrome b gene and morphological data, concluded that *S. parvidens* is an independent species of *S. lilium* (Iudica 2000). This information was reinforced by Velazco and Patterson (2013), based in the amplification of 3 mitochondrial loci (cytochrome b, hypervariable region HVRI section in Dloop, and ND2) and two nuclear genes (RAG1, and RAG2).

The phylogeographic analyses of some mitochondrial and nuclear loci (cytochrome b, hypervariable region HVRI section in Dloop, and RAG1) in *S. parvidens* shows that the species had its origin in the Early Pleistocene *c.* 1.84 Ma (95% CI: 2.553– 1.179). Despite the recent origin of the species, two haplogroups diverged in the Middle Pleistocene, *c.* 0.423 Ma (95% CI: 0.586–0.268): one is located in the Western Slope in Mexico, and the other in the Eastern Slope in Mexico and Central America (Fig. 4—Hernández-Canchola and León-Paniagua 2017).

To understand and analyze the genetic structure of its populations, 12 pairs of specific and polymorphic primers were designed to amplify microsatellite loci in *S. parvidens*; two of them are tetra-nucleotide, five are tri-nucleotide, and five are di-nucleotide (Gutiérrez et al. 2017).

CONSERVATION

Sturnira parvidens is considered abundant (Galindo-González et al. 2000; Estrada and Coates-Estrada 2001) and not currently in any risk category (Téllez-Girón and Amin 2014). Although the species is adaptable to habitat modifications (Cisneros et al. 2015; Briones-Salas et al. 2017) and forages in disturbed habitats, *S. parvidens* prefers to roost in mature forest. As fragmentation intensifies and forest patches become smaller and ever more impacted by human activity, *S. parvidens* is particularly vulnerable to local extinctions (Evelyn and Stiles 2003). The preservation of mature forest patches within human-dominated landscapes, and the preservation of isolated trees an live fences in disturbed areas, should be an important guiding principle for the conservation of this

species and the ecological services that it performs (Galindo-González et al. 2000; Evelyn and Stiles 2003; García-Morales et al. 2014). Forest management strategies can also change the speed of forest succession by affecting the arrival of seed disperser bats such as *S. parvidens* (Vleut et al. 2013).

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"Associate Editor was____ and ____ reviewed the synonymy[ies]. Editor was ___."

FIGURES

Fig.1.—A female of *Sturnira parvidens* from Rancho Hobonil, municipality of Tzucacab, Yucatán, Mexico. Photography taken in March, 2016. Used with permission of the photographer Martín Yair Cabrera-Garrido.

Fig.2.—A female of *Sturnira parvidens* from Presa Los Carros, municipality of Axochiapan, Morelos, Mexico. Photography taken in March, 2016. Used with permission of the photographer Yire Antonio Gómez-Jiménez.

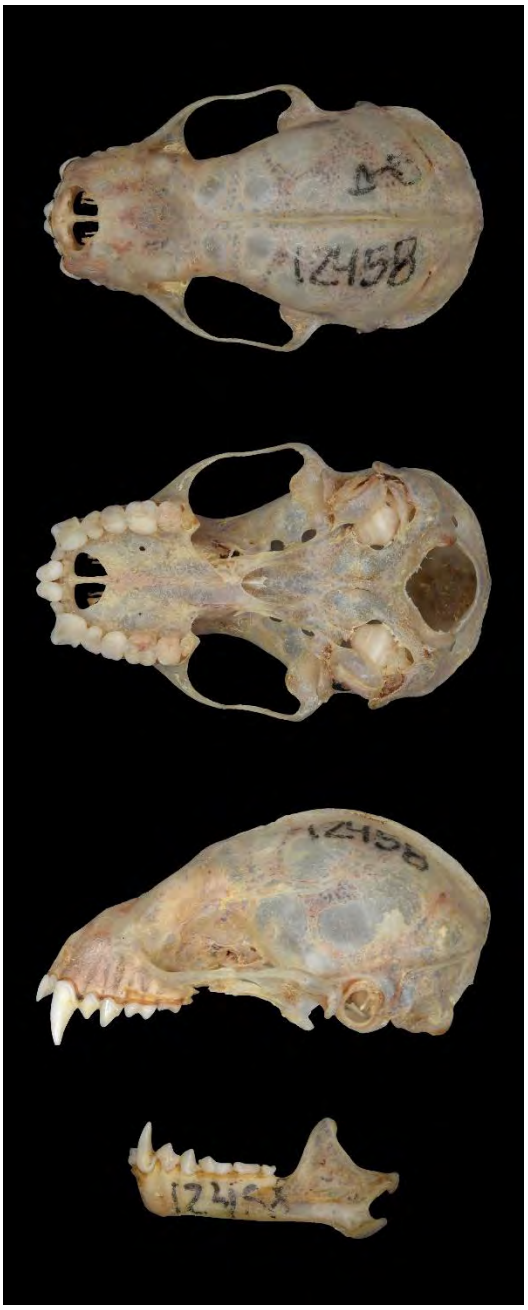

Fig.3.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Sturnira parvidens* (MZFC-M [Museo de Zoología, Facultad de Ciencias - UNAM] 12458) from Nizanda "Escolar", municipality Asunción Ixtaltepec, Oaxaca, Mexico. Greatest length of skull, excluding incisor is 22.62 mm. Used with permission of the photographer Sara Carolina Lucero-Verdugo.

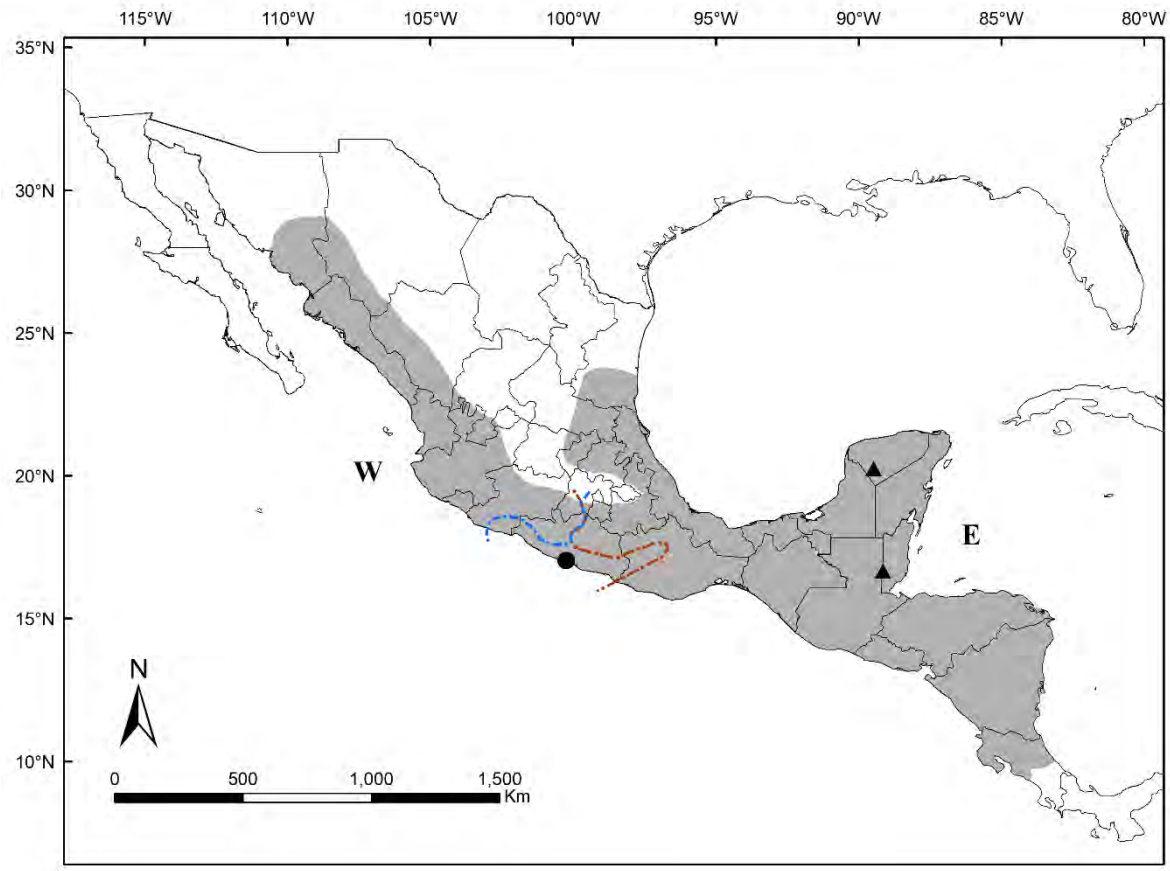

Fig.4.—Geographic distribution of *Sturnira parvidens*. The blue dotted line represents the western limit of E lineage, and the brown dotted line represents the eastern limit of the W lineage. Letters indicate genetic lineage ranges: E, Eastern Slope in Mexico and Central America; and W, Western Slope in Mexico. The point shows the type locality of *S. parvidens*. Triangles show the localities where fossils of *S. parvidens* have been found. Maps modified from Hernández-Canchola and León-Paniagua (2017).

CAPÍTULO 3.

Early differentiation within the highland Mesoamerican bat *Sturnira hondurensis* (Chiroptera: Phyllostomidae)

En preparación: Journal of Biogeography

Giovani Hernández-Canchola, Iván Hernández-Chávez, Nandadevi Cortés-Rodríguez y Livia León-Paniagua

Resumen

El género *Sturnira* es considerado el más diverso de todos los murciélagos frugívoros neotropicales. Sin embargo, aún no existe un consenso acerca de sus relaciones filogenéticas y los procesos evolutivos en este género, como en el caso de *Sturnira hondurensis* que recientemente fue reconocido como una especie independiente. Esta especie habita en las zonas montañosas de Mesoamérica, una región considerada como importante para analizar diversos procesos evolutivos. Analizamos las relaciones filogenéticas, la estructura filogeográfica, la demografía histórica, la variación morfológica y evaluamos la similitud del nicho climático de esta especie, para identificar los procesos evolutivos que posiblemente están involucrados en la evolución y actual distribución de *S. hondurensis*. Nuestros resultados sugieren que el ancestro de *S. hondurensis* y su especie hermana, *S. burtonlimi*, divergió en Mesoamérica posiblemente por la expansión y contracción de los bosques montanos durante las fluctuaciones climáticas del Pleistoceno. Estos eventos también promovieron la diferenciación genética de linajes al interior de *S. hondurensis*, ya que detectamos tres grupos geográficos dentro de la especie. Estos se encuentran separados por las tierras bajas del Istmo de Tehuantepec, la depresión del río

Balsas y el valle Pueble-Tlaxcala, pero la variación genética, morfológica y ambiental es sutil, por lo que representan grupos incipientes en un estadio muy temprano de diferenciación. Sin embargo, el grupo más diferente se localiza en el oeste de México, un área donde se han reconocido procesos de diversificación en muchos otros taxa. Destacamos la relevancia de la historia climática y la compleja topografía de la región en los procesos de diversificación de taxa montanos, como en el caso de muchos otros miembros del género *Sturnira*.

Article

Early differentiation within the highland Mesoamerican bat *Sturnira hondurensis* (Chiroptera: Phyllostomidae)

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ABSTRACT

The genus *Sturnira* is considered the most speciose of all Neotropical frugivorous bats. Nevertheless, there are still discrepancies about their relationships and evolutionary processes such as in *Sturnira hondurensis* that recently was recognized as an independent species. This bat inhabits highlands of Mesoamerica, a region considered important to study evolutionary processes. Here, we analyzed the phylogenetic relationships, phylogeographical structure, demographic history, morphological variation, and tested the conservatism of the climatic niche of this species in order to identify the evolutionary processes likely involved in the evolution and current distribution of *S. hondurensis*. Our results support that the ancestor of *S. hondurensis* and its sister species *S. burtonlimi* diverged in Mesoamerica, possibly by the expansion and contraction of montane forests during Pleistocene climatic fluctuations. These events also promoted the genetic differentiation of lineages within *S. hondurensis*, because we detected three geographic groups within the species. They are separated by the lowlands Isthmus of Tehuantepec, Balsas Basin and Puebla-Tlaxcala Valley, but the genetic, morphological and niche variation among them is subtle, so they may represent incipient groups in an early stage of differentiation. The most differentiated groups are located in western Mexico, a recognized area that have promoted the diversification processes in many other taxa. We highlight the relevance of the climatic history and complex topography of the region in the diversification processes of montane species, as in the case of many members of the genus *Sturnira*.

Keywords: Balsas Basin, Climatic niche divergence, Geometric morphometric, Isthmus of Tehuantepec, Nicaragua depression, Phylogeography, Puebla-Tlaxcala Valley.

INTRODUCTION

Mesoamerica, the Neotropical area from Mexico to Central America, is a hotspot of biodiversity and is considered one of the most intricate and complex areas in the world (Myers et al., 2000; León-Paniagua et al., 2007; Ruiz-Sanchez & Ornelas, 2014). Mesoamerica is considered as an important region to study evolutionary processes (Gutiérrez-García & Vázquez-Domínguez, 2013) due to the geographic position, complex tectonic and orogenic history, climate patterns, and abrupt topography that have acted together to generate its high biodiversity (Bryson et al., 2011).

Highlands of Mesoamerica are an important component of this region, because they include a complex assemblage of montane biotas, containing high endemism and biodiversity (Parra-Olea et al., 2012; Bryson et al., 2018). The oldest element of Mesoamerican highlands is the Sierra Madre Oriental that started its uprise since the Cretaceous and Paleocene (Graham, 1998), while the more recent important uprising in Mesoamerica occurred during transition of Pliocene – Pleistocene, in the Mountain ranges of Costa Rica and Panama (Gutiérrez-García & Vázquez-Domínguez, 2013). The sequential uprising of southern Mesoamerican geological elements concluded in the formation of the Isthmus of Panama, an event that allowed the interchange of biota of two continents previously isolated (North and South America; Gutiérrez-García and Vázquez-Domínguez 2012; Navarro-Sigüenza et al. 2017). On the other hand, the formation of the Panamanian isthmus interrupted the communication of the Atlantic and Pacific Oceans, changing the thermohyaline circulation, and promoting a new climactic pattern of glacial e interglacial oscillations (Haug & Tiedemann, 1998; Bartoli et al., 2005).

Mid-elevation and highland animals and plants were strongly affected by expansion and contraction of montane habitats during past climatic events (Sandoval et al., 2017), and during interglacial periods Mesoamerican lowlands represented a barrier that promoted diversification processes in multiple montane taxa (Ornelas et al., 2013; Ramírez-Barahona & Eguiarte, 2013). Nevertheless, although many species maintain the same biogeographical patterns, their specificity and levels of gene flow are idiosyncratic (Caviedes-Solis & Leaché, 2018).

One way to investigate the effects of these climatic events on the biota is through phylogeographic studies, which focus on the recent history of species by analyzing the geographical and temporal variation in genetic information within a single species or among closely related species (Avise, 2000). In addition to historical events, ecological processes also influence the evolutionary history of the species (Gutiérrez-Rodríguez et al., 2011; Morales et al., 2016), and significant environmental niche differentiations occurs in association with most speciation events (Warren et al., 2008). These analyses are useful in the detection of cryptic lineages in widespread morphologically conserved taxa, and for identifying boundaries of lineages at early stages of speciation (Wiens, 2004).

A good candidate to study the diversification processes in the region is the highland Mesoamerican yellow-shouldered bat *Sturnira hondurensis*. It belongs to genus *Sturnira*, the most speciose genus of frugivorous Neotropical bats, which comprises at least 21 species (Velazco & Patterson, 2013; Molinari et al., 2017). This genus includes three early-diverging Andean species (*S. aratathomasi*, *S. bidens*, and *S. nana*), a clade formed by 12 species that are usually found in montane forests (*S. adrianae*, *S. bogotensis*, *S. burtonlimi*, *S. erythromos*, *S. hondurensis*, *S. koopmanhilli*, *S. ludovici*, *S. magna*, *S. mordax*, *S.*

oporaphilum, *S. perla*, and *S. tildae*; hereafter clade A), and six species that inhabit lowland tropical forest and Caribbean islands (*S. angeli*, *S. bakeri*, *S. lilium*, *S. luisi*, *S. paulsoni*, and *S. parvidens*; hereafter clade B).

Sturnira hondurensis inhabits highlands of Mesoamerica and was originally described in contrast with *S. ludovici* as a smaller species, with lower incisors deeply bilobed instead of simple (Goodwin, 1940). Nevertheless, *S. hondurensis* was synonymized to *S. ludovici* by Hershkovitz (1949) because he noted that some Colombian *S. ludovici* with bilobate lower incisors wear these teeth, and lose this characteristic with the age. Molecular and morphological reviews of genus *Sturnira* supported evidence to recognize *S. hondurensis* as an independent species, close related to *S. burtonlimi*, *S. adrianae*, *S. ludovici* and *S. oporaphilum* (hereafter the *S. oporaphilum* clade; Iudica 2000; Velazco and Patterson 2013; Velazco and Patterson 2014; Molinari et al. 2017); and the timetree analysis suggests that *S. hondurensis* originated *c.* 2.5 Ma, after the emergence of Panamian isthmus (Velazco & Patterson, 2013). However, there is no consensus on inter-specific relationships of *S. hondurensis* and its related species (Iudica, 2000; Velazco & Patterson, 2013; Rojas et al., 2016; Molinari et al., 2017), and there are inconsistences about the geographic boundaries of them (e.g. Téllez-Girón 2014).

There are two recognized subspecies within this taxon: *Sturnira hondurensis occidentalis*, found in western Mexico from Sinaloa to Nayarit, and *S. hondurensis hondurensis* located in all other areas where this species is found (Jones & Phillips, 1964). *S. h. occidentalis* is smaller, has a shorter and more abruptly elevated rostrum, a broader skull and is paler than *S. h. hondurensis* (Jones & Phillips, 1964). Iudica (2000) only analyzed Central American populations of *S. h. hondurensis*, and found evidence of

multiple genetic lineages that were not been previously detected in morphological studies (Jones & Phillips, 1964).

As *S. hondurensis* evolved in Mesoamerica after all its relevant geographic features were formed, we suspect that *S. hondurensis* recent evolutionary processes that produces the subspecies or multiple genetic lineages within the species, were consequence of climatic oscillation occurred during Pleistocene. We used phylogeographic, niche divergence and morphometric analyses to understand the historical and ecological factors involved in the evolutionary history of this species. Our goals were (1) to clarify the phylogenetic position of *S. hondurensis*, (2) to analyze if there is congruence among genetic, ecologic and morphologic analyses, (3) and to analyze if the historical or ecological factor are involved in the diversification process of this species.

MATERIALS AND METHODS

Taxon sampling and molecular protocols

We collected 20 specimens of *S. hondurensis* in various states in Mexico following Mexico's wildlife legislation (SEMARNAT SGPA/DGVS/11606/08257/06724). All material is deposited in the Mammal collection of the Zoology Museum, UNAM (Facultad de Ciencias – Universidad Nacional Autónoma de México, Mexico City, Mexico, MZFC-M). We used additional tissue samples of *S. hondurensis* and related species that are hosted in the following scientific collections: MZFC-M; Royal Ontario Museum, Toronto, Canada (ROM); Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional – Instituto Politécnico Nacional, Durango, Mexico (CIIDIR-D); El Colegio de la Frontera Sur

– Unidad San Cristóbal, San Cristóbal, Mexico (ECO-SC-M); and Museo de Zoología – Universidad de Costa Rica, San José, Costa Rica (MZUCR). We also included 1 uncatalogued wing tissue sample that was collected in the field.

We extracted total DNA using the Qiagen DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA, USA). Through polymerase chain reaction (PCR), we amplified the mitochondrial loci *cytochrome b* (*cyt-b*), the *hypervariable D-loop region I* (*D-loop*), and the nuclear *recombination activating gene 1* (*RAG1*) using the primers reported by Velazco and Patterson (2013). A negative control was included during each round of PCR. Each PCR had a final reaction volume of 12.5 µL and contained 7.325 µL of H_20, 1.25 µL Buffer [10x], 0.825 µL of dNTP's Mix [2mM], 0.75 µL of $MgCl_2$ [25mM], 0.625 µL of each primer [10µM], 0.1 µL of Taq polimerase [5u/µL] (Vivantis Technologies Sdn. Bhd., Selangor, Malaysia), and 1 µL of DNA stock. The PCR profile included 3 minutes of initial denaturation at 95°C, followed by 35 cycles of 30 seconds of denaturation at 95°C, 1 minute of annealing at 48° - 49°C (*cyt-b*), 58°C (*RAG1*), and 59°C (*D-loop*); and 2 minutes for extension at 72°C. Finally, we included a step of 8 minutes of final extension at 72°C. With 1.5 µL of each PCR, we visualized these products through an electrophoresis in agarose gels with TAE [1x], stained with GelRed (Biotium Inc., Fremont, CA, USA). 5 µL of PCR products were cleaned with 1 µL of ExoSAP-IT (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA) using the next protocol: 30 minutes at 37°C, followed by 15 minutes at 80°C. The samples were cycle-sequenced employing 4.4 µL H_20, 3.4 µL Buffer, 0.60 µL of primer [10µM], 0.6 µL of ABI PRISM Big Dye v. 3.1 (Applied Biosystems, Foster City, CA, USA), and1 µL of cleaned template. The cycle-sequencing profile included 1 minute of initial denaturation at 96°C, followed by 25 cycles of 10 seconds of

denaturation at 96°C, 5 seconds of annealing at 50°C, and 4 minutes for extension at 60°C. These products were purified through an EtOH-EDTA precipitation protocol and were read in an ABI 3730 automatic sequencer (Applied Biosystems, Foster City, CA, USA). The DNA sequences were edited and aligned using MEGA 6 (Tamura et al., 2013) and FINCHTV 1.4 (Patterson et al., 2004), conducting a visual inspection of all the sequences.

Phylogenetic analyses

To analyze the phylogenetic relationships between *S. hondurensis* and related species, we included the sequences available of genus *Sturnira* (Velazco & Patterson, 2013; Molinari et al., 2017), and used *Vampyriscus bidens* as the out-group. Only in the case of *S. aratathomasi* we combined the sequences of two different individuals (ROM 70874: *cyt-b*; and FMNH 189778: *D-loop*), following Velazco and Patterson (2013).

For the nuclear gene *RAG1* we obtained the allelic phases using the coalescent-based Bayesian method of the Phase algorithm (Stephens et al., 2001; Stephens & Donnelly, 2003) in DNASP 5.10 (Librado & Rozas, 2009). We employed 10,000 iterations, sampling data every 10 iterations, with a burn-in of 1,000. We allowed recombination and set an output probability threshold of 0.9, and we used the resulting highest probability haplotypes. After being phased, we tested the evidence of recombination using TOPALI 2.5 (Milne et al., 2004). We did not find significant DSS peaks and we used the complete allelic phases in further analyses.

We conducted five different phylogenetic analyses: one for each molecular marker (*cyt-b*: n = 278; *D-loop*: n = 269; *RAG1*: n = 462), plus two analyses of concatenated

matrices (*cyt-b*/*D-loop*: n = 280; *cyt-b*/*D-loop*/*RAG1*: n = 280). Data were concatenated using one of the phased nuclear gene copies chosen at random for each individual (McCormack et al., 2011). In PARTITIONFINDER 2 (Guindon et al., 2010; Lanfear et al., 2017) we determined the best substitution model for the each best partition of the dataset, using the corrected Akaike Information Criterion and the greedy algorithm (Lanfear et al., 2012).

Bayesian analyses were performed in MRBAYES 3.2.3 (Ronquist et al., 2012) employing the MCMC algorithm. We used the partition and substitution models calculated previously: *cyt-b*: GTR+I+Γ; *D-loop*: GTR +I+Γ; *RAG1*: SYM+I+Γ; *cyt-b*/*D-loop*: GTR+I+Γ; and *cyt-b*/*D-loop*/*RAG1*: GTR+I+Γ. We used 3 hot and 1 cold chains, in two independent runs of 20 million generations (40 millions in the case of nuclear gen), sampling data every 2,000 iterations. The final topology was obtained using a majority rule consensus tree, and considering a burn-in of 10%. We checked the convergence of our results and a good sampling (ESS > 200) in TRACER 1.6.

In MEGA 6 we calculated the genetic distances in *cyt-b* and *D-loop*, using the pairwise deletion option and the Kimura 2-parameter model (Kimura, 1980). We used these parameters with the goal of continuity and comparability with previous works (Baker & Bradley, 2006).

Phylogeographic structure analyses

For each locus, we analyzed the geographic structure of the variable genetic sites in GENELAND (Guillot et al., 2012). We used this Bayesian method because it considers

genetic data and their geographic coordinates to identify genetic discontinuities between populations and because GENELAND includes an option to work with haplotype data. We also used the option for codominant markers to analyze the allelic phases in *RAG1*. We tested the occurrence of different populations from 1 to 10, using 5 million generations with a thinning of 250, a true spatial model, uncorrelated genetic frequencies, and a value of 0.02° as coordinate uncertainty that correspond with the largest distance traveled by *S. hondurensis* (Cortés-Delgado & Sosa, 2014). We did a burn-in of 30 % in mitochondrial loci and of 25 % in the nuclear one, we watched the convergence of the results over 10 independent runs, and chose the run with the highest likelihood value.

We tested for phylogeographic structure in the mitochondrial molecular markers. We calculated the values of genetic differentiation over all populations (G_{ST}), as well as the values of differentiation considering genetic distance (N_{ST}) using PERMUT (Pons & Petit, 1996). We tested the significance of the results with 10,000 permutations. N_{ST} values significantly greater than G_{ST} values were taken to corroborate a phylogeographic structure.

We generated two mitochondrial haplotype networks in NETWORK 5, using the Median Joining algorithm (Bandelt et al., 1999). Due to our relatively large data set, we followed the recommendations of the authors to visualize results using the star contraction (set to 5) and we eliminated the unnecessary median vectors using the MP option.

We analyzed hierarchical percentages of variation considering the recognized subspecies and a geographical division. We constructed standard AMOVAs in ARLEQUIN 3.5 (Excoffier & Lischer, 2010). We used a matrix of pairwise differences according to the Kimura 2-parameter model, using 10,000 permutations to test the significance of our results.

Genetic diversity and demographic analyses

In DNASP 5.10, the following genetic measures were calculated for each locus: number of segregating sites (*S*), number of haplotypes (*h*), haplotype diversity (*Hd*) and nucleotide diversity (π). To explore the demographic history of the species, we calculated Fu's *Fs* (Fu, 1997), *R2* (Ramos-Onsins & Rozas, 2002) and raggedness index (*r*; Rogers and Harpending 1992). The significance of these values were assessed using the coalescent algorithm implemented in DNASP 5.10, using 1000 replicas.

Coalescent analysis using isolation with migration

We used coalescent analysis to study the divergence history of these geographic groups detected in previous analyses. The program Isolation with Migration (IMA2; Hey and Nielsen 2007) jointly estimates demographic parameters to obtain posterior probability distributions from unliked genes. In addition, this new implementation of IM estimates demographic parameters for multiple populations and it is described in Hey (2010a; 2010b). These parameters offer the opportunity of capturing the dynamics of a population during the early stages of differentiation (Hey, 2005). The model estimates the following parameters that are then scaled to the per-locus mutation rate: effective population sizes (θn = population n, θA = ancestral population), migration rates (*m*), and the time of population splitting (*t*). The inherited scalar was defined as 0.25 for mitochondrial and 1 for nuclear loci. To improve the mixing of Markov chains, we ran multiple heated chains and monitored the autocorrelation and ESS (effective sample sizes) estimates. To convert the

parameter estimates into biologically informative values, we assumed an average generation time of 7.5 months and substitution rates of *cyt-b* = 0.0147 s/s/Ma (95% CI [confidence interval]: 0.0106–0.0233); *Dloop* = 0.0434 s/s/Ma (95% CI: 0.0313–0.0685); and *RAG1* = 0.0060 s/s/Ma (95% CI: 0.0043–0.0094), reported in *S. parvidens* (Hernández-Canchola & León-Paniagua, 2017). These mutational rates were provided in the IM input file and used to convert the parameter estimates into biological informative values. In addition, we used IMFIG to visualize their phylogenetic history as a figure.

Morphometric analyses

As intraspecific morphological differences reported in *S. hondurensis* are based on Euclidean distances and skull structures verbally described, we analyzed statistically the size and shape of these bats. We took pictures of dorsal, lateral and ventral views of the skulls of adult individuals of *S. hondurensis* and other related species as external groups. The specimen vouchers are hosted in the following scientific collections: MZFC-M, ROM, MZUCR, Colección Nacional de Mamíferos of the Instituto de Biología – Universidad Nacional Autónoma de México, Mexico City, Mexico (CNMA), and in the Field Museum of Natural History, Chicago (FMNH).

To analyze the shape using geometric morphometric analyses, we collected Cartesian coordinates from anatomical points and curvatures (landmarks and semi-landmarks) using MAKEFAN8 (Sheets, 2006a) and TPSDIG 2.30. We analyzed five different configuration of coordinates that are related with intra or inter specific morphological differences reported in *S. hondurensis*, and in other *Sturnira* or phyllostomid frugivorous

bats (Jones and Phillips 1964; Jarrín-V and Kunz 2011; Velazco and Patterson 2014; López-Aguirre et al. 2015). They were dorsal view of the skull, lateral braincase, lateral rostrum, glenoid fossa and posterior edge of the palatine (Fig. S1 in Appendix S2).

To discard the effects not related with shape and obtain a size estimator (centroid size), each configuration was subjected to an generalized procrustes analyses using COORDGEN8 (Sheets, 2006b), and semi-landmarks were aligned and confined as a curve with SEMILAND8 (Sheets, 2006c).

We obtained the Procrustes distances in CVAGEN8 (Sheets, 2006d) to analyze whether there is a relationship between them and the genetic distances using a Mantel Test calculated in the R package VEGAN 2.5-1 (Oksanen et al., 2018). With the same Procrustes distances, in PAST 3.19 (Hammer et al., 2001) we constructed clusters using the UPGMA algorithm with 900 bootstraps.

The following analyzes were done only with geographic groups within *S. hondurensis*. In PAST 3.19 we tested differences in centroid size among sexes and geographic groups using Mann-Whitney and Kruskal-Wallis tests followed by a Dunn *post hoc* comparison (all values were not under homocedasticity, Levene test $p < 0.05$). To test whether the shape variation was explained by differences in centroid size (allometric effect), in REGRESS8 (Sheets, 2006e) we did a multivariate regression of the shape on the size estimator. In each configuration, we tested differences of the shapes among geographic groups and sexes using an Procrustes ANOVA analysis in the R package GEOMORPH 3.0.5 (Adams et al., 2017), followed by a pairwise comparison through a Goodall's *F* test conducted in TWOGROUP8 (Sheets, 2006f) with 900 bootstraps. To visualize the differences detected in shape, in CVAGEN8 we constructed a canonical variate analysis (CVA), and in

the significant canonical axes, we constructed the thin plate spline deformation grids in PAST 3.19.

Additionally, in TMORPHOGEN8 (Sheets, 2006g) we obtained de Euclidian distance of two lineal measurements that reflect the long and wide of the skull. In PAST 3.19 and in each measurement we searched differences among sexes and geographic groups, followed by *post hoc* analyses.

Comparison of climatic niches

We tested niche similarity among geographic groups using the method proposed by Broennimann et al. (2012). This method includes a multivariate analysis of the environmental space that is gridded in *r* x *r* cells of unique environments, then an occurrence density surface in environmental space is created using a kernel density method, considering the occupancy and availability of environments. We used these surfaces to calculate the amount of climatic niche overlap between genetic lineages, and if they are more or less similar than expected under a null model of random distribution of points (niche similarity test; Warren et al. 2008). We chose niche similarity test because it is sense to test biogeographic and evolutionary hypotheses (Hu et al., 2016). We used nine Bioclim variables at a resolution of 30 arc-seconds (Hijmans et al., 2005) that are important limiting factors of Neotropical bats (Stevens, 2011). Variables that characterized temperature were: annual mean, seasonality, maximum in the warmest month, and minimum in the coldest month and isothermality. Variables that characterized precipitation were: total annual, total in wettest month, total in driest month, and seasonality. We used the occurrence data

available in VertNet (http://portal.vertnet.org accessed on February 27th, 2018) and the geographic information of all samples used for the genetic analyses. For definition of background environment, we used a buffer of 0.5° in the registers obtained. These analyses were performed in the R package ECOSPAT 2.1.1 (Broennimann et al., 2016) and the niche tests were executed with 1000 iterations.

RESULTS

Molecular sample sizes

We analyzed genetic data of one sample of *Vampyriscus bidens*, and 280 individuals of the genus *Sturnira*: 77 samples correspond to *S. aratathomasi*, *S. bidens*, *S. nana*, and species from clade B. In the clade A we analyzed two individuals of *S. ludovici*, seven of *S. adrianae*, seven of *S. oporaphilum*, five of *S. burtonlimi*, 146 of *S. hondurensis*, and 36 individuals that correspond to other species in clade A. We obtained a total of 1140 bp for *cyt-b*; 422 bp in *D-loop*; and 1072 bp for *RAG1*. All sequences are available in Genbank (Table S1 in Appendix S1).

Phylogenetic analyses of the *Sturnira oporaphilum* clade

The concatenated phylogenetic hypotheses show that *S. hondurensis* (from Mexico to Honduras) is sister to *S. burtonlimi* (Costa Rica and Panama) (Fig. 1). The clade composed by *S. ludovici* (Ecuador), *S. adrianae* (Venezuela) and S. *oporaphilum* (Ecuador and Peru) is sister to *S. hondurensis* – *S. burtonlimi* clade (Fig. S2 in Appendix S3). Within *S. hondurensis* we detected six genetic lineages, all of them supported with high probability

values. Two of them are located mainly east of the Isthmus of Tehuantepec but some specimens inhabits in central Mexico (eastern clades: E1 – 2); another lineage only inhabits at the east of the Isthmus of Tehuantepec (eastern clade: E3). Two other lineages are endemic to central Mexico (central clades: C4 – 5). Finally, another linage is located in western Mexico (western clade: W6) (Figs. 1 – 2). Nevertheless, the relationships among these six clades are not completely resolved. In both concatenated Bayesian analyses, the clade E1 is sister to all other clades with high support value. The construction obtained using mitochondrial and nuclear loci shows that the next divergent event produced the clade E2 (with high posterior probability value), and then the clade E3 (with low posterior probability value). Clade E3 is sister to a polytomy that includes all other Mexican clades: C4 – 5 and W6, nevertheless, this relationship does not has a high posterior probability value. In general, the phylogenetic constructions based in individual loci show the same genetic lineages described anteriorly; nevertheless, the relationships are less clear, and even in the case of RAG1, samples of *S. hondurensis* where mixed with all other *Sturnira* species in clade A, except *S. magna* (Fig. S3 in Appendix S3).

The genetic distances in *cyt-b* among *S. hondurensis* and related species ranged from 3.96 % (*S. adrianae – S. oporaphilum*) to 6.43 % (*S. oporaphilum – S. hondurensis* [East of Tehuantepec Isthmus]), whereas in *D-loop* ranged from 4.93 % (*S. ludovici – S. hondurensis* [central Mexico]) to 6.7 % (*S. oporaphilum – S. hondurensis* [central Mexico]). Among *S. hondurensis*, in *cyt-b* the genetic distances ranged from 1.02 % (central Mexico – western Mexico) to 1.58 % (East of Tehuantepec Isthmus – western Mexico), whereas in *D-loop* from 2.8 % (central Mexico vs western Mexico) to 3.55 % (East of Tehuantepec Isthmus – western Mexico) (Table S3 in Appendix S3).

Phylogeographic structure within *Sturnira hondurensis*

GENELAND Bayesian analyses displayed some differences among molecular markers. In the case of *cyt-b*, there are three genetic/geographic groups, two of them are mainly found at the east of the Isthmus of Tehuantepec and some in central Mexico, whereas the third group is found in central and western Mexico. In the case of *D-loop* there are four groups, two in the east of the Isthmus of Tehuantepec and central Mexico, other in central Mexico, and another in western Mexico. In the case of the nuclear loci *RAG1* there are two groups: between western Mexico and east of the Isthmus of Tehuantepec there is a clear genetic division, whereas in central Mexico there are a mixture of the two groups (Fig. S4 in Appendix S3).

In phylogeographical structure tests, we obtained lower values of G_{ST} (*cyt-b* = 0.062 standard error, SE: 0.025; *D-loop* = 0.067 SE: 0.027) than N_{ST} values (*cyt-b* = 0.228 SE: 0.046; *D-loop* = 0.243 SE: 0.064). After permutations we corroborate that N_{ST} values were significantly higher than G_{ST} ($p < 0.01$), indicating phylogeographical structure among *S. hondurensis* populations.

In both mitochondrial networks we detected haplogroups that are similar to the six genetic lineages obtained in phylogenetic analyses. In the nuclear network, E1 – 2 and C4 lineages have exclusive alleles, whereas other alleles are almost exclusive of haplogroup W6. Nevertheless, all other alleles are shared indistinctly among linages (Fig. 2).

The higher percentage of variation among groups was detected using the geographical division of samples (*cyt-b* = 30.22 %; *D-loop* = 30.34 %). The division was

East of Tehuantepec Isthmus, central Mexico and western Mexico. This percentage of variation among groups was higher than using the recognized subspecies division (*cyt-b* = 24.99 %; *D-loop* = 26.31 %), or even using a range extension of subspecies *S. h. occidentalis* considering the distribution of haplogroup W6 located in western Mexico (*cyt-b* = 28.63 %; *D-loop* = 30.5 %). Nevertheless, in all cases the higher percentage of variation was found within populations (ranges *cyt-b* = 56.74 – 62.15 %; *D-loop* = 57.2 – 63.52 %) (Table 1).

Genetic diversity and demographic analyses

We detected 86 and 99 mitochondrial haplotypes (*cyt-b* and *D-loop* respectively), and 35 nuclear alleles in *S. hondurensis*. The percentage of variable sites in *cyt-b* was 8.77 %, in *D-loop* was 14.79 %, and in *RAG1* was 2.79 %. In mitochondrial loci we detected high levels of haplotype diversity, but in the nuclear locus we found low and high levels of haplotype diversity. In all cases the nucleotide diversity values were low. Fu's *Fs*, *R2* and *r* indices showed higher evidence of demographic expansion in eastern and central groups than in western group. Nevertheless, in all cases the signal of demographic expansion is low (Table 2).

Coalescent analysis using isolation with migration

The IMA2 analysis (Fig. 3) showed that eastern *S. hondurensis* diverged from Mexican populations *c.* 74,534 years ago (95% HPD [highest posterior density interval]: 53,808 – 100,840 years), whereas Mexican populations of *S. hondurensis* from west and center split

c. 71,345 years ago (95% HPD: 49,025 – 95,260 years). We only detected recent migration from east to center population (3.8 migrants per generation).

Morphometric analyses

We analyzed morphometric data from 5 skulls of *S. mordax*, 8 of *S. oporaphilum*, 13 of *S. burtonlimi* and 166 samples of *S. hondurensis* (Table S2 in Appendix S1). In almost all pairwise comparisons, we found evidences of correlation between genetic and Procrustes distances ($r > 0.69$, $p < 0.05$), except in the posterior edge of the palatine (both loci), the dorsal view (*cyt-b*) and braincase (*D-loop*). In cluster analyses, in the cases of the dorsal view, braincase and rostrum we detected the three geographic groups within *S. hondurensis* as a phenetic group. The glenoid fossa of eastern and central group are more similar to *S. burtonlimi*, and in the case of the posterior edge of the palatine the western group is more similar to *S. burtonlimi*. In many cases the central group was more similar to the eastern group and the west group is the most dissimilar (Fig. S5 in Appendix S3).

In the majority of the configurations, we found that the centroid sizes of the eastern groups are the largest, and in some cases the centroid sizes of western group are the smallest (Fig. S6 in Appendix S3). These differences are significant in dorsal view, braincase, glenoid fossa and palatine between east vs west and central groups (Table 3, Table S4 in Appendix S3). In three configurations we found a significant correlation between the centroid size and the shape (dorsal view, braincase and glenoid fossa, $p < 0.05$), nevertheless any percentages of variation related with the shape was superior to 5.7 %, so we do not find evidence of a relevant allometric effect on shape.

The Procrustes ANOVA showed that there are not differences in the shape of the rostrum and glenoid fossa among groups. Nevertheless, the shapes of the dorsal view of the skull, the braincase and the posterior edge of the palatine showed subtle differences among groups (Table 3). With the Goodall's *F*, the CVA and the thin plate spline deformation grids (Fig. 4, Fig. S7 and Table S5 in Appendix S3), we detected that the most effective traits that shows differences within *S. hondurensis* groups are the dorsal view of the skull and the posterior edge of the palatine, because in any sex is possible to differentiate the western vs central and eastern groups. The shape of the braincase is different among all groups but only in males. Besides, there are sexual dimorphism in the dorsal view, the braincase and glenoid fossa (Table 3).

In the case of Euclidean distances involving the length and width of the skull, we found that the east group animals are largest, whereas the west group are smaller (Fig. S8 in Appendix S3). These differences are significant in the length of the skull among all geographic groups, except in females of west vs center group; but in the width there are only differences in males of the west vs east and center groups (length: Shaphiro-Wilk test $p > 0.05$, Levene test $p < 0.05$; width: Shaphiro-Wilk test $p > 0.05$, Levene test $p > 0.05$). We detected sexual dimorphism in the length, but not in the width of the skull (Table 4).

Comparison of climatic niches

We initially obtained 880 depurated occurrence records from Vertnet and our data. After discarding records within 1 Km of each other, we analyzed 202 occurrence data (*S. hondurensis* western = 53, *S. hondurensis* central = 76, *S. hondurensis* eastern = 73). The

first two components of the PCA performed for climatic niche comparison accounted the next total environmental variation west – center 67.81%, west – east 70.15%, and center – east 65.52% (Fig. S9 in Appendix S3). The western climatic niche is almost completely included in the central niche, and the overlap between center – east niches was higher than in west – east (Fig. 5). Nevertheless, only in the case of center – east niches we found that they were more similar than random in two reciprocal directions ($p < 0.05$).

DISCUSSION

Sturnira oporaphilum (Tschudi, 1844), *S. ludovici* (Anthony, 1924), and *S. hondurensis* (Goodwin, 1940) were recognized species, until Hershkovitz (1949) lumped them and other species into *S. ludovici*. This action obscured the diversity of *Sturnira* bats for many years (Iudica, 2000), but the confusion began to be resolved by molecular studies of the genus (Iudica, 2000; Velazco & Patterson, 2013), leading to subsequent descriptions of *S. burtonlimi* (Velazco & Patterson, 2014), *S. adrianae* (Molinari et al., 2017), or the phylogeographic analysis of *S. parvidens* (Hernández-Canchola & León-Paniagua, 2017). Molecular information has proved to be important in *Sturnira* bats because the relationships among species apparently cannot be clarified using a morphological analyses (Pacheco & Patterson, 1991; Iudica, 2000). In addition, morphological variation within the genus is subtle, and in some cases the characters used to diagnose different species have proven to be inconsistent (Jarrín-V & Clare, 2013; Sánchez & Pacheco, 2016).

The *Sturnira oporaphilum* clade

Our analyses agree with previous studies that supported the monophyly of a clade composed by *S. adrianae*, *S. burtonlimi*, *S. hondurensis*, *S. ludovici* and S. *oporaphilum*, however, there are conflicts about their phylogenetic relationships (Iudica 2000; Velazco and Patterson 2013; Molinari et al. 2017). Using three mitochondrial and two nuclear molecular markers, Velazco and Patterson (2013) showed that *S. hondurensis* is sister of *S. burtonlimi*, *S. ludovici* and *S. oporaphilum*. On the other hand, with partial *cyt-b* was proposed that the sister clades of *S. ludovici* are *S. adrianae* + *S. oporaphilum* and *S. burtonlimi* + *S. hondurensis* (Molinari et al., 2017). These differences must be related with different molecular markers used in each study and the inclusion of *S. adrianae* samples. Here we analyzed in detail the phylogenetic position of *S. hondurensis* and related species, and for first time a study included samples of all morphologic and genetic reported groups within *S. hondurensis*, representing the most complete geographic representation of this species, and our hypothesis is congruent with Iudica (2000), who used partial *cyt-b* and morphological information.

In the *S. oporaphilum* clade, the latest described species was *S. adrianae* (Molinari et al., 2017), which has the smallest genetic distances among species. Considering that all species in the *S. oporaphilum* clade live in mountain habitats (i.e. continental islands), their genetic distances (Baker & Bradley, 2006), geographic ranges and morphological differences (Velazco and Patterson 2014; Molinari et al. 2017), we agree in recognize all of them as independent species. The Mesoamerican species *S. burtonlimi* and *S. hondurensis* show an allopatric distribution. Bats in the *S. oporaphilum* clade from Costa Rica and Panama must be considered as *S. burtonlimi*, whereas specimens from Mexico to northern Nicaragua as *S. hondurensis*. In South America, we found that *S. adrianae*, *S. ludovici* and

S.oporaphilum are distributed from North to South through the Andes. Nevertheless, their geographic boundaries are not completely clear, and to understand their distribution is necessary a re-identification of all South American bats in the *S. oporaphilum* clade hosted in scientific collections, following Velazco and Patterson (2014) and Molinari et al. (2017).

Our results sustain a pair of sister lineages, the South American clade and the Mesoamerican clade. This hypothesis support only one event of migration between South and Central America, dated *c.* 2.5 Ma (Velazco & Patterson, 2013), when the ancestor of *S. burtonlimi* and *S. hondurensis* was able to cross the Panamanian isthmus at the beginning of the Pleistocene. This time coincides with one pulse of the Great American Biotic Interchange, in which many other Neotropical species crossed towards Central America (Arteaga et al., 2012). After the ancestor established in Mesoamerica, it started a diversification process that originated to *S. hondurensi*s and *S. burtonlimi*. It is possible that from Costa Rican and Panamanian region occurred an expansion into Northern Central America, possibly related with forest expansion and contraction (Hoffmann & Baker, 2003). A possible subsequent isolation and diversification of these species during the Pleistocene was likely due to volcanic activity, uplift processes, climate changes, or lowland floods (Gutiérrez-García & Vázquez-Domínguez, 2012). Both Mesoamerican species are geographically separated by the Nicaraguan depression, and these lowlands have promoted genetic differentiation in other mammals as the felids *Leopardus pardalis* and *Leopardus wiedii* (Eizirik et al., 1998), the rodent *Ototylomys phyllotis* (Gutiérrez-García & Vázquez-Domínguez, 2012), the short-tailed bat *Carollia sowelli* (Hoffmann & Baker, 2003), and birds (Arbeláez-Cortés et al. 2010, and references therein).

Intraspecific differentiation in *S. hondurensis*

Previous studies evidenced different Central American lineages within *S. hondurensis* (Iudica, 2000; Molinari et al., 2017), that may represent different species or subspecies (Iudica, 2000). We extended the sampling from Mexico to Central America, detecting more than two genetic lineages within *S. hondurensis*. Lowlands of the Tehuantepec Isthmus, the Puebla-Tlaxcala Valley and the Balsas Basis could act as geographic barriers in this montane species.

We found subtle variation among these intraspecific groups. In genetics, central – western groups are the most similar, whereas the eastern – western groups are the most divergent. In the case of the shapes of the skull the western group is the most different, and the eastern – central groups are similar (Fig. 6). We also found that the largest specimens are found at the east of the Isthmus of Tehuantepec and the smallest in western Mexico. Finally, the eastern – central groups have the most similar climatic niches, whereas the western – eastern groups have most dissimilar niches.

The most evident variation was previously detected when the subspecies *S. h. occidentalis* was described (Jones & Phillips, 1964), but we propose that the geographic range of this lineage extends through Sierra Madre Occidental and the Transmexican Volcanic Belt, reaching Puebla-Tlaxcala Valley. On the other hand, there are none reports about morphological differences between central and eastern lineages, possibly because its great morphological similarity. We concluded that is easier to distinguish *S. hondurensis* from western Mexico and East of Tehuantepec Isthmus, but excluding the geographic range and using only one methodology, it is more difficult to differentiate specimens from central Mexico.

De Queiroz (2007) proposed that different types of evidence in addition to the time elapsed since the differentiation occurred, are elements necessaries to determine if lineages under study can be considered as different species. In some cases we detected subtle variation among geographic groups, but it was not possible to differentiate them in all comparisons, in special those involving the cryptic central group. In part this low resolution may be the result of very recent divergence times. We cannot consider them independent species, but we suspect they are incipient groups in an early stage of differentiation. Our study highlights the importance of including a complete sampling, because if we had not included samples from Central Mexico, we may have concluded the occurrence of two well differentiated groups (west and east), obscuring the diversification processes within *S. hondurensis*.

As in other Mesoamerican montane taxa, the isolation of populations in multiple habitat refuges apparently played an important role in the genetic divergence followed by population expansion (Parra-Olea et al., 2012; Bryson et al., 2018). We suggest that Pleistocene climatic changes promoted the geographic distribution and genetic differentiation of groups within this species, because *S. hondurensis* is associate to montane forests, and this bat must had followed the vegetation that suffered expansion ranges to lowlands during glacial periods, and contraction ranges during interglacial periods (Ramírez-Barahona & Eguiarte, 2013). We suggest that during forest expansions *S. hondurensis* was able to colonize new habitats from Central America to Mexico, but during the forest contractions, its populations were isolated by lowlands, and started multiple events of differentiation. This hypothesis is supported by the stepping stone colonization model suggested in Mexican highlands (Mastretta-Yanes et al., 2015), besides the time of

divergence among groups supports this hypothesis, because only strong interglacial periods promote the differentiation of groups (Jaramillo-Correa et al., 2008).

The Isthmus of Tehuantepec represents the most frequent shared break among montane taxa (Barber & Klicka, 2010; Ornelas et al., 2013). These lowlands allowed the differentiation the eastern group, nevertheless, it effect was dual, because in some cases it acted as a barrier and in other as a connector (Cortés-Rodríguez et al., 2013), allowing the presence of eastern haplotypes in central Mexico. Explanation is an incomplete sorting lineage (Avise, 2000), but we found evidences of genetic flow, suggesting that this isthmus allowed migration of individuals after the differentiation of the eastern group, but this process only occurred northward.

The similarity niche test shows similar niches between east and central groups. Nevertheless, we hypothesize that other ecological traits or biological interactions may be involved in the differentiation of their niches, suggesting a hypothetical eastern niche that include the central niche and restrict the migration southwards. There is evidence that when one niche is contained in another, the migration only occurs in one direction because the individuals of the smallest niche has not survive in different conditions (Arteaga et al., 2011).

On the other hand, the central and western groups are divided by the lowlands of the Balsas Basin and the Puebla-Tlaxcala Valley. The Balsas Basin separates the Sierra Madre del Sur from the Transmexican Volcanic Belt (Marshall & Liebherr, 2000) and this depression has promoted genetic differentiation in other mammals (Sullivan et al., 1997, 2000; Amman & Bradley, 2004). Our calculations suggest that the divergence between central and western groups was related to an interglacial climatic events, however other

geological events such as recent volcanism in the Transmexican Volcanic Belt could have promoted this genetic structuration (Mastretta-Yanes et al., 2015), likely as in the Puebla-Tlaxcala Valley.

The geographical features are the main factors that have promoted the differentiation of central and western lineages due to central niche includes the western climatic niche, notwithstanding the niche tests rejected the similarity of west vs center and east. This dissimilarity is relevant in the process of lineage differentiation, because historical colonization and environmental suitability are important factors that shape the distribution of species in time and space (Di Cola et al., 2017). We detected that specimens from western Mexico inhabits in more extreme temperatures, and areas with more seasonality, such as the western populations of *S. parvidens* (Hernández-Canchola & León-Paniagua, 2017). In this congeneric frugivorous bat that mainly roosts in tress (Fenton et al., 2000), the western niche differentiation is likely related with stress tolerance, instead of changes in feed and roosts because plants depend more of rainfall (Hernández-Canchola & León-Paniagua, 2017). Nevertheless, skulls of individuals from the western group are more rounded and smaller and this is related with an increase of the bite force (Nogueira et al., 2009), and modifications in palate are thought to underlie feeding specialization in bats (Sorensen et al., 2014). So we suspect that in western Mexico there may exist environmental factors that affect the plants consumed by these bats. On the other hand, we do not find evidences of differentiation in the rostrum among groups, as was previously mentioned in the description of *S. h. occidentalis* (Jones & Phillips, 1964), highlighting the relevance of statistical interpretation of morphological dissimilarity, instead of qualitative judgments of character variation (Jarrín-V & Kunz, 2011). Nevertheless, our results are

similar to Jones and Phillips (1964) in detecting that eastern specimens are the largest, following a reverse ecological trend (larger individuals in higher latitudes) called Bergamann's Rule converse, as has been reported in *Carollia perspicillata*, another frugivorous phyllostomid bat (de Barros et al., 2014)

We detected lower signals of demographic expansion in western Mexico, possibly as a consequence of its heterogeneous topography, that may have allowed the persistence of more stable populations during past climatic events (Hernández-Canchola & León-Paniagua, 2017). In this sense, we highlight the relevance of western Mexico in the diversification processes of Mexican mammal, because it contains many endemism (Ceballos, 2014).

In an analysis about the evolution and biogeography of New World noctilionoid bats, Rojas et al. (2016) suggested that the speciation rates in phyllostomid bats do not depend on any geological period, but are clade dependent. Nevertheless, we agree with Hernández-Canchola and León-Paniagua (2017), who suggested that lineage accumulations plus Pleistocene climatic oscillations molded together the diversification and distribution of *Sturnira* bats. Besides, in the montane taxa such as *S. hondurensis*, landscape discontinuity is a very important factor that determines population structure, where habitat fragmentation represent a barrier to dispersal (Caviedes-Solis & Leaché, 2018). In this sense, the geographic features of the Neotropical region have been a relevant factors in the diversification processes of genus *Sturnira* because this topography have differentiated more mountain than lowland species, in the most speciose genus of frugivorous Neotropical bats (Velazco & Patterson, 2013; Molinari et al., 2017).

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TABLES AND FIGURES

Table 1. Results of the analyses of molecular variance (AMOVA) using mtDNA markers. Each AMOVA correspond to (a) *S. h. occidentalis* (Sinaloa – Nayarit) and *S. h. hondurensis* (all other samples); (b) *S. h. occidentalis* (Sinaloa – Estado de México) and *S. h. hondurensis* (all other samples); (c) East of the Tehuantepec Isthmus, Central Mexico and Western Mexico.

		(a)		(b)		(c)	
Molecular marker	Soruce of variation	Pv	Fc	Pv	Fc	Pv	Fc
cyt-b	Among groups	24.99	0.250	28.63	0.286	30.22	0.302
	Among populations within groups	17.53	0.234	14.63	0.205	7.63	0.109
	Within populations	57.48	0.425	56.74	0.433	62.15	0.379
D-loop	Among groups	26.31	0.263	30.5	0.305	30.34	0.303
	Among populations within groups	15.54	0.211	12.29	0.177	6.14	0.088
	Within populations	58.15	0.418	57.2	0.428	63.52	0.365

Pv: Percentage of variation; Fc: *F* coefficients. All *F* coefficients are significant values ($p < 0.05$).

Table 2. Results of genetic diversity and demographic analyses for each molecular marker. See text for details.

Loci	Group	n	S	h	Hd	Hd(sd)	π	π(sd)	*Fs*	*R2*	*r*
cyt-b	*S. hondurensis*	146	100	86	0.985	0.004	0.0121	0.00036	**-53.304**	0.067	**0.004**
1140 bp	Eastern Tehuantepec	50	70	33	0.974	0.011	0.01294	0.00036	-7.184	0.099	0.010
	Central Mexico	60	59	40	0.97	0.012	0.00997	0.00076	**-16.154**	0.091	**0.007**
	Western Mexico	36	19	15	0.937	0.017	0.00327	0.00018	-4.150	0.094	0.047
D-loop	*S. hondurensis*	146	62	99	0.993	0.002	0.02876	0.00069	**-89.396**	0.095	**0.002**
419 bp	Eastern Tehuantepec	50	52	44	0.995	0.005	0.03111	0.00105	**-28.329**	0.118	0.008
	Central Mexico	60	44	39	0.979	0.008	0.02315	0.00164	**-17.806**	0.106	**0.006**
	Western Mexico	36	17	17	0.946	0.017	0.00815	0.00071	**-7.117**	0.097	**0.024**
RAG1	*S. hondurensis*	238	30	35	0.891	0.011	0.00262	0.00013	**-19.564**	0.046	0.026
1072 bp	Eastern Tehuantepec	74	22	26	0.901	0.024	0.00274	0.00022	**-15.774**	0.065	**0.016**
	Central Mexico	104	20	18	0.885	0.016	0.0024	0.00019	-5.315	0.063	0.034
	Western Mexico	60	9	6	0.454	0.077	0.00124	0.00027	0.033	0.074	0.292

Boldface numbers indicate significant values ($p < 0.05$ in *R2* and *r*; and $p < 0.02$ in *Fs*).

Table 3. Results of the Mann-Whitney (*Z*) and Kruskal-Wallis (*H*) analyzes of centroid size and Procrustes – ANOVA of the shapes of the skulls. Boldface numbers indicate significant values.

		CS		Procrustes - ANOVA		
		Z / H	p	*F*	*Z*	p
Dorsal	Sexes	-2.687	**0.007**	7.635	3.938	**0.001**
	Groups	40.720	**0.000**	5.943	4.569	**0.001**
	Interaction			2.083	2.062	**0.016**
Braincase	Sexes	-0.681	0.496	2.771	2.078	**0.013**
	Groups	49.350	**0.000**	2.918	2.653	**0.003**
	Interaction			1.673	1.467	0.069
Rostrum	Sexes	-0.338	0.736	2.726	1.617	0.061
	Groups	0.506	0.777	1.967	1.446	0.085
	Interaction			0.429	-1.214	0.887
Glenoid fossa	Sexes	-0.434	0.665	3.747	2.039	**0.014**
	Groups	60.430	**0.000**	2.074	1.435	0.077
	Interaction			0.687	-0.309	0.619
Palatine	Sexes	-0.652	0.514	1.966	1.194	0.124
	Groups	37.520	**0.000**	10.148	3.803	**0.001**
	Interaction			1.779	1.300	0.100

Table 4. Results of the Mann-Whitney (*Z*), Kruskal-Wallis (*H*) and ANOVA (*F*) followed by Dunn and Tukey (*Q*) *post-hoc* analyzes of the measurements of the skulls. Boldface numbers indicate significant values.

		Length		Width	
		Z / *H*	p	*F*	p
	Sexes	-2.866	**0.004**	2.862	0.093
	Groups	61.680	**0.000**	10.620	**0.000**
	Interaction			5.104	**0.007**
	Post-hoc		p	*Q*	p
Females-west	Females-center		0.205	1.509	0.823
Females-west	Females-east		**0.000**	1.486	0.831
Females-center	Females-east		**0.001**	3.268	0.147
Males-west	Males-center		**0.000**	4.340	**0.021**
Males-west	Males-east		**0.000**	7.337	**0.000**
Males-center	Males-east		**0.000**	3.900	0.050
Females-west	Males-west		0.969	2.441	0.421
Females-center	Males-center		**0.005**	3.334	0.133
Females-east	Males-east		**0.013**	3.281	0.144

Figure 1. Bayesian inferences that show the phylogenetic relationships of *S. hondurensis* and related species, showing the posterior probability values at each node: (a) hypothesis with both mitochondrial loci, (b) hypothesis with three molecular markers (two mitochondrial and the nuclear loci). The height of enclosing triangles is proportional to the number of samples they contain.

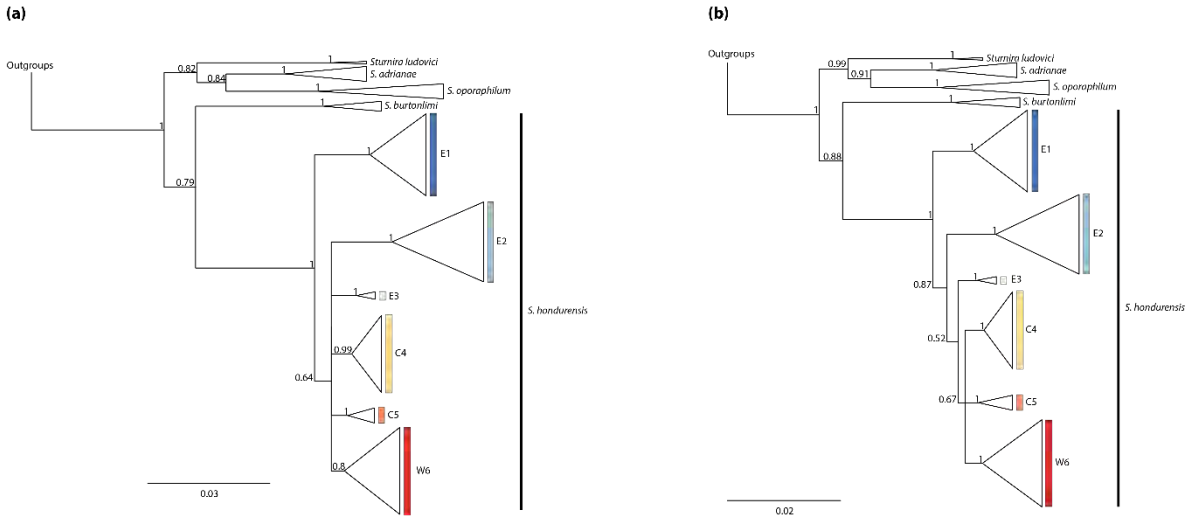


Figure 2. Phylogeographic structure in *S. hondurensis*. The colors represent the same genetic linages described in Fig. 1. The map shows the distribution of each genetic lineage, and the bar size is proportional to the number of samples per locality. The dotted black line represent the geographic range of this species. At the right, the networks for each molecular marker: (a) *cyt-b*, (b) *D-loop*, and (c) *RAG1*. The circle is proportional to the frequency of haplotypes or alleles, and the line length to the number of mutations. TI: Tehuantepec Isthmus; PTV: Puebla-Tlaxcala Valley; BB: Balsas Basin.

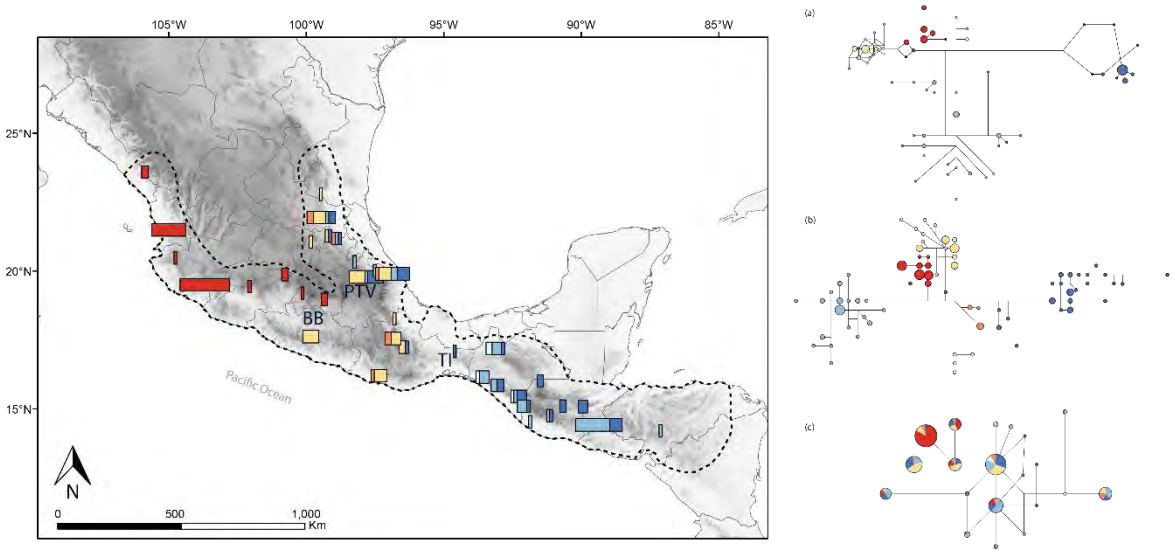


Figure 3. History of the three different populations of *Sturnira hondurensis* (east, central and west). Population size is represented as width along the horizontal axis and time is represented on the vertical axis. The curved arrows show migration (2NM) and asterisks identify curves that are statistically significant by the test of Nielsen and Wakeley (2001): *p ≤ 0.05, **p ≤ 0.01, and ***p ≤ 0.001.

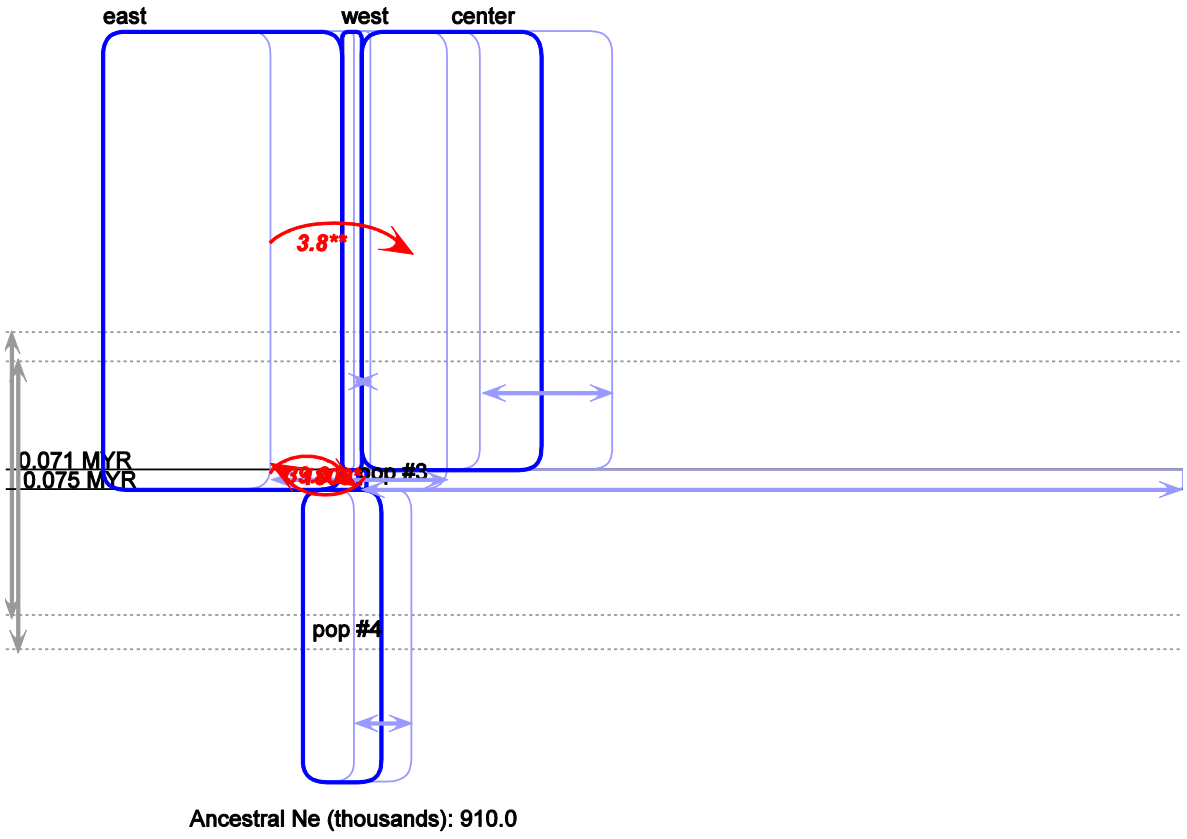


Figure 4. Shape variation of dorsal skull and lateral braincase. Scatter plots of CVAs and deformation grids of shape changes along the first canonical axis. (a) Dorsal view – females, (b) dorsal view – males, (c) lateral braincase – females, (d) lateral braincase – males. In CVAs: blue = east, yellow = central, red = west groups. In deformation grids, the color represents the degree of variation in the shapes, red indicates expansion whereas blue contraction.

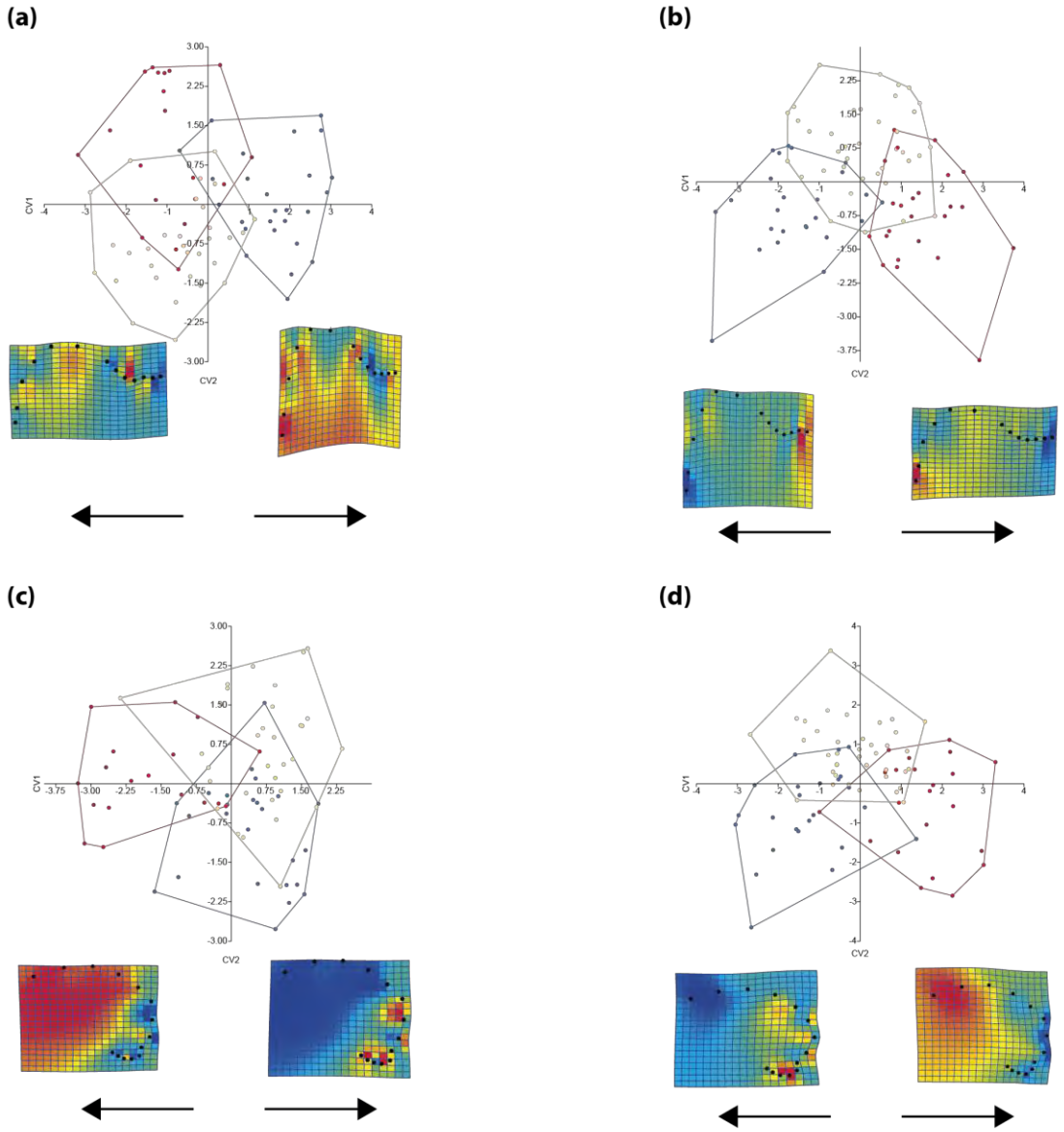


Figure 5. Pairwise comparison of the climatic niche along the first two axes of the PCA, between geographic groups within *S. hondurensis*. The red color represent the group of Western Mexico, the yellow is the group of Central Mexico, and the blue is the group of the East of the Tehuantepec Isthmus. The solid and dashed lines illustrate the 100% and 50% of the available environment. In the first and second columns, the gray shading shows the density of the occurrences of each group by cell. The third column shows the overlap in each comparison.

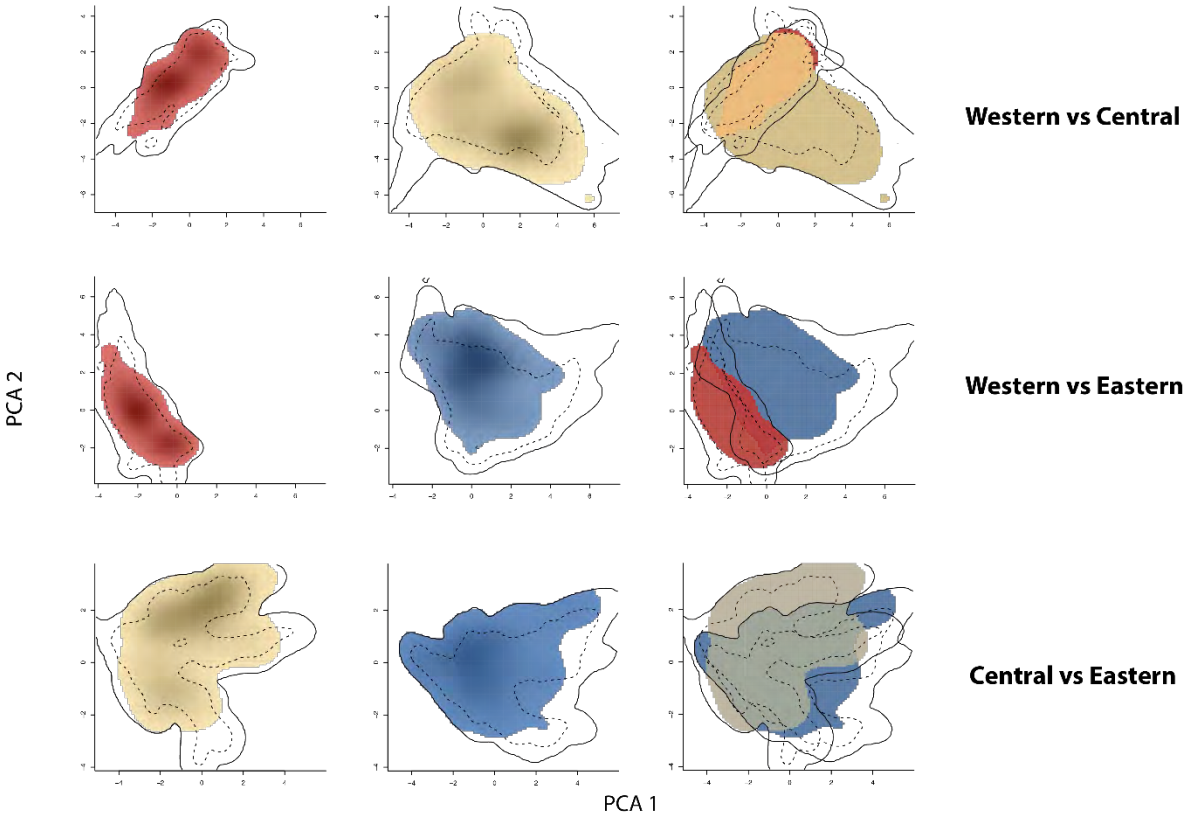
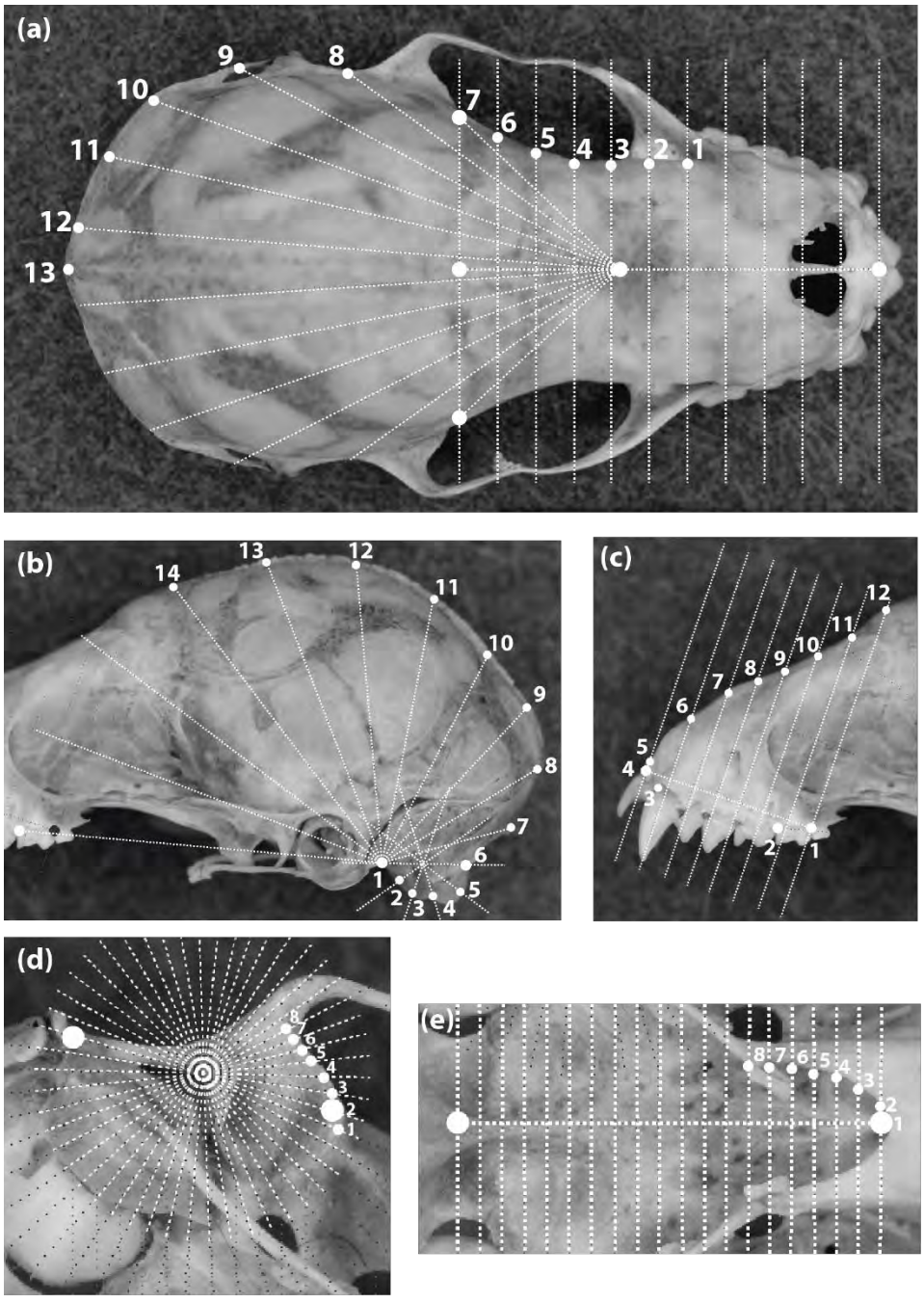


Figure 6. Skulls of three groups within *S. hondurensis*. From left to right: west, central and east groups. MZFC-M 14980 from Nayarit, Mexico; MZFC-M 11261 from Veracruz, Mexico; MZFC-M 10015 from Chiapas, Mexico. Bar scale = 10 mm.

APPENDIX S2

Figure S1. Set of landmarks and semi-landmark configurations designed to register the shape of the (a) dorsal view, (b) lateral braincase, (c) lateral rostrum, (d) glenoid fossa and (e) posterior edge of palatine.



APPENDIX S3

Table S3. Genetic distance matrix for species of the genus *Sturnira* using the Kimura 2-parameters model. Above the diagonal the values for *D-loop*, and below the diagonal the values for *cyt-b*.

	Vamp	S_bid	S_nan	S_ara	S_ns3	S_ang	S_lui	S_pau	S_lil
Vamp		0.1783		0.1772	0.2113	0.2139	0.2016	0.1953	0.1878
S_bid	0.1431			0.1171	0.1356	0.1321	0.1309	0.1199	0.1230
S_nan	0.1445	0.0865							
S_ara	0.1602	0.1155	0.1033		0.1083	0.1189	0.1118	0.0989	0.1018
S_ns3	0.1467	0.0930	0.0752	0.0611		0.0562	0.0627	0.0471	0.0709
S_ang	0.1545	0.0925	0.0794	0.0660	0.0232		0.0585	0.0465	0.0634
S_lui	0.1516	0.0948	0.0726	0.0676	0.0191	0.0219		0.0394	0.0608
S_pau	0.1555	0.0900	0.0750	0.0640	0.0215	0.0235	0.0192		0.0622
S_lil	0.1644	0.1048	0.0917	0.0886	0.0590	0.0677	0.0588	0.0628	
S_bak	0.1583	0.1162	0.0872	0.0858	0.0553	0.0656	0.0584	0.0626	0.0612
S_par	0.1555	0.1069	0.0910	0.0806	0.0506	0.0557	0.0539	0.0563	0.0526
S_til	0.1588	0.1139	0.0924	0.0823	0.0758	0.0783	0.0764	0.0770	0.0833
S_per	0.1549	0.0936	0.0828	0.0824	0.0647	0.0734	0.0685	0.0694	0.0745
S_koo	0.1532	0.1015	0.0881	0.0825	0.0594	0.0698	0.0675	0.0636	0.0711
S_mor	0.1628	0.1002	0.0870	0.0836	0.0714	0.0683	0.0725	0.0749	0.0686
S_mag	0.1618	0.1294	0.1117	0.1029	0.0815	0.0858	0.0840	0.0841	0.0888
S_bog	0.1535	0.1006	0.0974	0.0939	0.0721	0.0676	0.0752	0.0776	0.0755
S_ery	0.1642	0.1101	0.0922	0.0865	0.0707	0.0763	0.0725	0.0763	0.0745
S_lud	0.1493	0.1059	0.0857	0.0884	0.0715	0.0731	0.0712	0.0708	0.0754
S_adr	0.1600	0.0962	0.0852	0.0872	0.0619	0.0721	0.0698	0.0647	0.0715
S_opo	0.1645	0.1053	0.0907	0.0923	0.0774	0.0723	0.0817	0.0772	0.0789
S_bur	0.1692	0.1033	0.0888	0.0955	0.0775	0.0800	0.0825	0.0831	0.0849
S_honE	0.1615	0.1029	0.1017	0.0957	0.0787	0.0838	0.0844	0.0847	0.0772
S_honC	0.1621	0.0994	0.1007	0.0953	0.0752	0.0806	0.0810	0.0812	0.0753
S_honW	0.1617	0.0944	0.0986	0.0937	0.0746	0.0782	0.0805	0.0808	0.0750

Table S3. Cont.

	S_bak	S_par	S_til	S_per	S_koo	S_mor	S_mag	S_bog	S_ery
Vamp	0.2120	0.1954	0.2520	0.2131	0.2002	0.1973	0.2029	0.2131	0.2112
S_bid	0.1417	0.1339	0.1756	0.1272	0.1543	0.1253	0.1190	0.1369	0.1531
S_nan									
S_ara	0.1240	0.1113	0.1487	0.1060	0.1182	0.1120	0.0934	0.1282	0.1149
S_ns3	0.0819	0.0779	0.1464	0.0984	0.1077	0.0940	0.0925	0.1110	0.1325
S_ang	0.0688	0.0662	0.1499	0.0881	0.0990	0.0922	0.0835	0.1211	0.1381
S_lui	0.0744	0.0737	0.1447	0.0808	0.0971	0.0845	0.0862	0.1242	0.1257
S_pau	0.0611	0.0652	0.1375	0.0731	0.0989	0.0757	0.0743	0.1182	0.1181
S_lil	0.0798	0.0720	0.1357	0.0909	0.0821	0.0836	0.0927	0.0966	0.1350
S_bak		0.0695	0.1625	0.0948	0.1017	0.1034	0.0801	0.1350	0.1370
S_par	0.0347		0.1454	0.0872	0.0764	0.0681	0.0833	0.1162	0.1294
S_til	0.0970	0.0850		0.1132	0.1472	0.1212	0.1345	0.1403	0.1280
S_per	0.0789	0.0787	0.0664		0.0803	0.0583	0.0664	0.1168	0.0955
S_koo	0.0828	0.0721	0.0668	0.0615		0.0548	0.0885	0.1262	0.1238
S_mor	0.0886	0.0775	0.0660	0.0525	0.0441		0.0658	0.0914	0.0902
S_mag	0.0988	0.0977	0.0916	0.0662	0.0702	0.0744		0.1014	0.1005
S_bog	0.0882	0.0808	0.0757	0.0638	0.0617	0.0609	0.0654		0.1245
S_ery	0.0831	0.0789	0.0702	0.0544	0.0633	0.0664	0.0792	0.0643	
S_lud	0.0821	0.0727	0.0781	0.0644	0.0681	0.0588	0.0774	0.0619	0.0770
S_adr	0.0823	0.0731	0.0800	0.0648	0.0615	0.0548	0.0735	0.0663	0.0718
S_opo	0.0870	0.0833	0.0879	0.0682	0.0658	0.0664	0.0884	0.0742	0.0833
S_bur	0.0939	0.0839	0.0857	0.0596	0.0649	0.0618	0.0800	0.0724	0.0779
S_honE	0.0898	0.0799	0.0922	0.0674	0.0803	0.0682	0.0849	0.0745	0.0845
S_honC	0.0897	0.0792	0.0884	0.0658	0.0793	0.0647	0.0826	0.0719	0.0801
S_honW	0.0886	0.0785	0.0878	0.0646	0.0788	0.0644	0.0810	0.0692	0.0801

Table S3. Cont.

	S_lud	S_adr	S_opo	S_bur	S_honE	S_honC	S_honW
Vamp	0.2042		0.2070	0.2128	0.2005	0.1977	0.1943
S_bid	0.1225		0.1376	0.1257	0.1150	0.1098	0.1093
S_nan							
S_ara	0.1075		0.1093	0.1142	0.1025	0.1024	0.0910
S_ns3	0.1246		0.1231	0.1073	0.1031	0.1022	0.1011
S_ang	0.1110		0.1151	0.1122	0.1037	0.0999	0.1002
S_lui	0.1102		0.1020	0.1009	0.0964	0.0978	0.0984
S_pau	0.0978		0.0974	0.0966	0.0843	0.0843	0.0836
S_lil	0.1125		0.1050	0.1100	0.0958	0.0915	0.0955
S_bak	0.1114		0.1184	0.1132	0.1090	0.1092	0.1066
S_par	0.0967		0.0979	0.1074	0.0951	0.0956	0.0863
S_til	0.1416		0.1493	0.1349	0.1386	0.1344	0.1370
S_per	0.0825		0.0829	0.0821	0.0741	0.0768	0.0845
S_koo	0.1157		0.0976	0.1133	0.0990	0.1031	0.0936
S_mor	0.0862		0.0797	0.0895	0.0721	0.0737	0.0676
S_mag	0.0893		0.0958	0.0929	0.0883	0.0922	0.0848
S_bog	0.1168		0.1331	0.1191	0.1085	0.1071	0.1043
S_ery	0.1207		0.1247	0.1161	0.1072	0.1086	0.0988
S_lud			0.0578	0.0586	0.0532	0.0493	0.0495
S_adr	0.0450						
S_opo	0.0512	0.0396		0.0593	0.0645	0.0670	0.0626
S_bur	0.0573	0.0418	0.0571		0.0553	0.0566	0.0583
S_honE	0.0600	0.0480	0.0643	0.0534		0.0343	0.0355
S_honC	0.0580	0.0449	0.0626	0.0506	0.0145		0.0280
S_honW	0.0579	0.0451	0.0620	0.0474	0.0158	0.0102	

Table S4. *Post-hoc* Dunn analyzes of centroid size of skulls. Boldface numbers indicate significant p values.

		Dorsal	Braincase	Rostrum	Glenoid fossa	Palatine
Females-west	Females-center	0.432	0.864	0.673	0.362	0.306
Females-west	Females-east	**0.006**	**0.000**	0.225	**0.000**	**0.002**
Females-center	Females-east	**0.028**	**0.000**	0.061	**0.000**	**0.000**
Males-west	Males-center	**0.000**	0.149	0.578	0.247	0.094
Males-west	Males-east	**0.000**	**0.000**	0.063	**0.000**	**0.038**
Males-center	Males-east	**0.001**	**0.003**	0.128	**0.000**	**0.000**
Females-west	Males-west	0.652	0.664	0.444	0.893	0.326
Females-center	Males-center	**0.021**	**0.048**	0.367	0.704	0.571
Females-east	Males-east	**0.002**	0.390	**0.017**	0.563	0.942

Table S5. Goodall's *F* test analyzes of shapes of the skulls. Boldface numbers indicate significant values.

		Dorsal			Braincase			Rostrum			Glenoid fossa			Palatine		
		d	*F*	p	d	*F*	p	d	*F*	p	d	*F*	p	d	*F*	p
F-west	F-center	0.008	5.190	**0.001**	0.008	1.610	0.133	0.014	2.280	0.096	0.023	0.850	0.407	0.024	5.240	**0.007**
F-west	F-east	0.008	4.850	**0.001**	0.009	1.870	0.102	0.012	1.610	0.171	0.035	1.610	0.162	0.017	3.330	**0.027**
F-center	F-east	0.006	3.610	**0.003**	0.007	1.390	0.203	0.006	0.400	0.751	0.018	0.570	0.631	0.011	1.380	0.229
M-west	M-center	0.007	4.110	**0.001**	0.010	2.310	**0.036**	0.011	1.470	0.187	0.031	1.550	0.177	0.038	13.220	**0.001**
M-west	M-east	0.009	5.730	**0.001**	0.013	3.850	**0.004**	0.009	0.880	0.444	0.039	1.670	0.169	0.034	9.350	**0.001**
M-center	M-east	0.005	1.820	0.084	0.011	2.770	**0.016**	0.008	0.810	0.477	0.036	1.970	0.132	0.012	1.670	0.178
F-west	M-west	0.004	0.960	0.436	0.007	1.100	0.331	0.011	1.300	0.244	0.040	1.880	0.116	0.010	0.700	0.522
F-center	M-center	0.007	5.260	**0.001**	0.008	2.100	0.073	0.011	1.920	0.121	0.024	1.210	0.287	0.012	1.800	0.159
F-east	M-east	0.009	5.440	**0.001**	0.011	2.940	**0.017**	0.006	0.410	0.782	0.041	2.030	0.107	0.017	3.440	**0.033**
F-west	M-center	0.008	5.230	**0.001**	0.007	0.930	0.427	0.018	4.040	**0.012**	0.038	2.340	0.079	0.035	13.020	**0.001**
F-west	M-east	0.011	7.400	**0.001**	0.013	3.180	**0.014**	0.014	2.410	0.080	0.069	5.250	**0.008**	0.029	8.620	**0.001**
F-center	M-west	0.007	4.940	**0.001**	0.007	1.500	0.160	0.013	1.920	0.124	0.028	1.230	0.273	0.029	6.390	**0.001**
F-center	M-east	0.008	5.440	**0.001**	0.013	4.880	**0.001**	0.008	0.850	0.419	0.053	4.150	**0.022**	0.007	0.480	0.673
F-east	M-center	0.008	6.540	**0.001**	0.011	3.310	**0.006**	0.011	1.520	0.174	0.013	0.280	0.867	0.019	4.590	**0.010**
F-east	M-west	0.008	4.570	**0.001**	0.008	1.600	0.154	0.009	1.000	0.352	0.029	1.120	0.324	0.020	3.470	**0.024**

F = females; M = males; d = distance among means.

Figure S1. Geographic distribution of samples of S. hondurensis and related species used in this work.

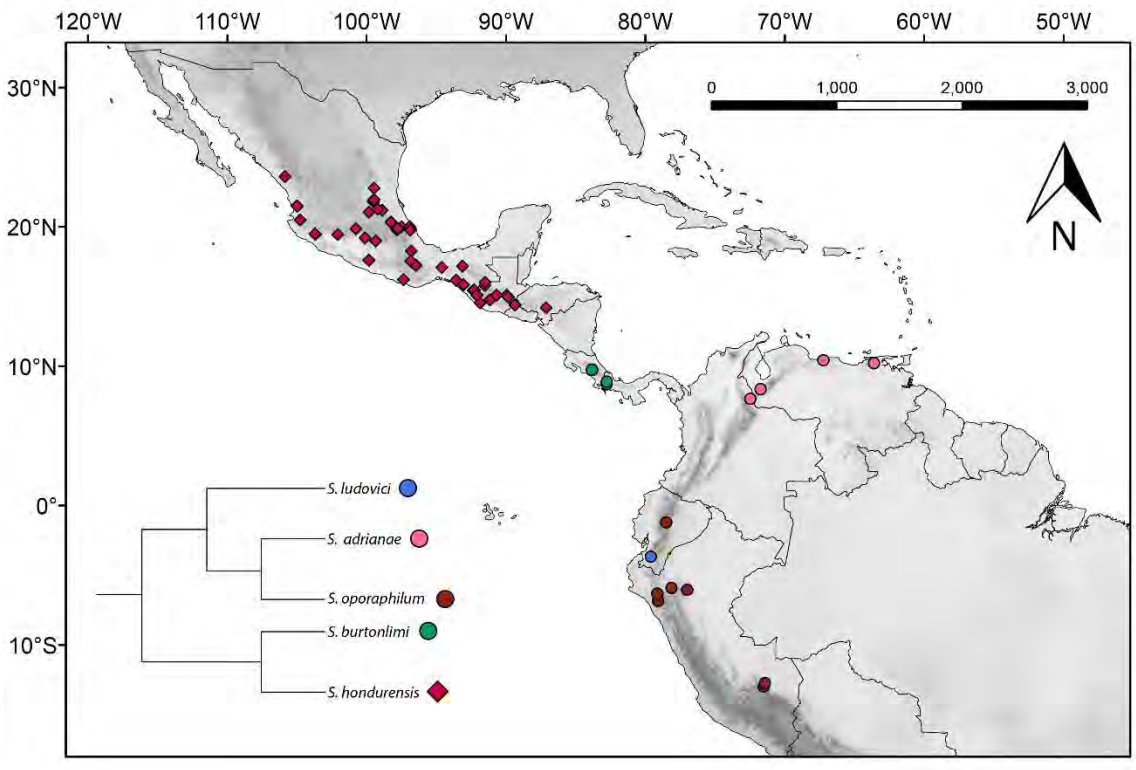


Figure S2. Bayesian inferences that shows the phylogenetic relationships of *S. hondurensis* and related species, showing the posterior probabilities at each clade: (a) *cyt-b*, (b) *D-loop*, (c) *RAG1*. The height of enclosing triangles is proportional to the number of samples they contain.

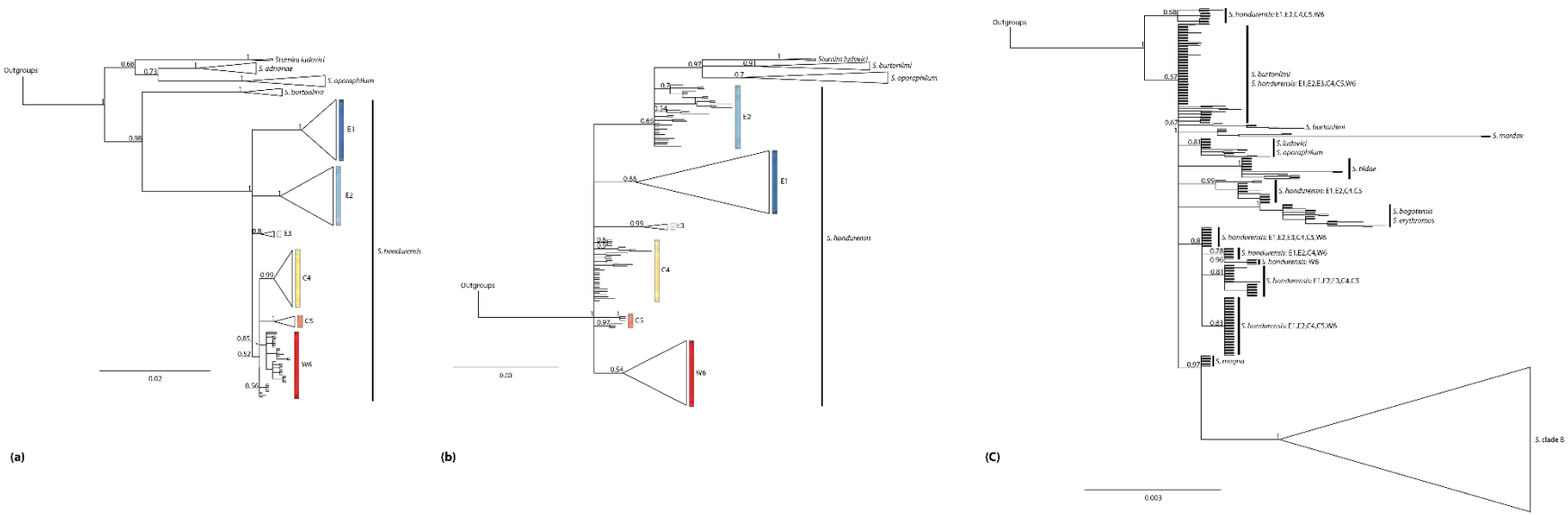


Figure S3. Assignment probabilities for each individual to the groups detected in GENELAND. (a) *cyt-b* K = 3, (b) *D-loop* K = 4, (c) *RAG1* K =2. The letters inside the circles indicated the geographic origin of each sample, E: East of Tehuantepec Isthmus; C: Central Mexico; W: Western Mexico.

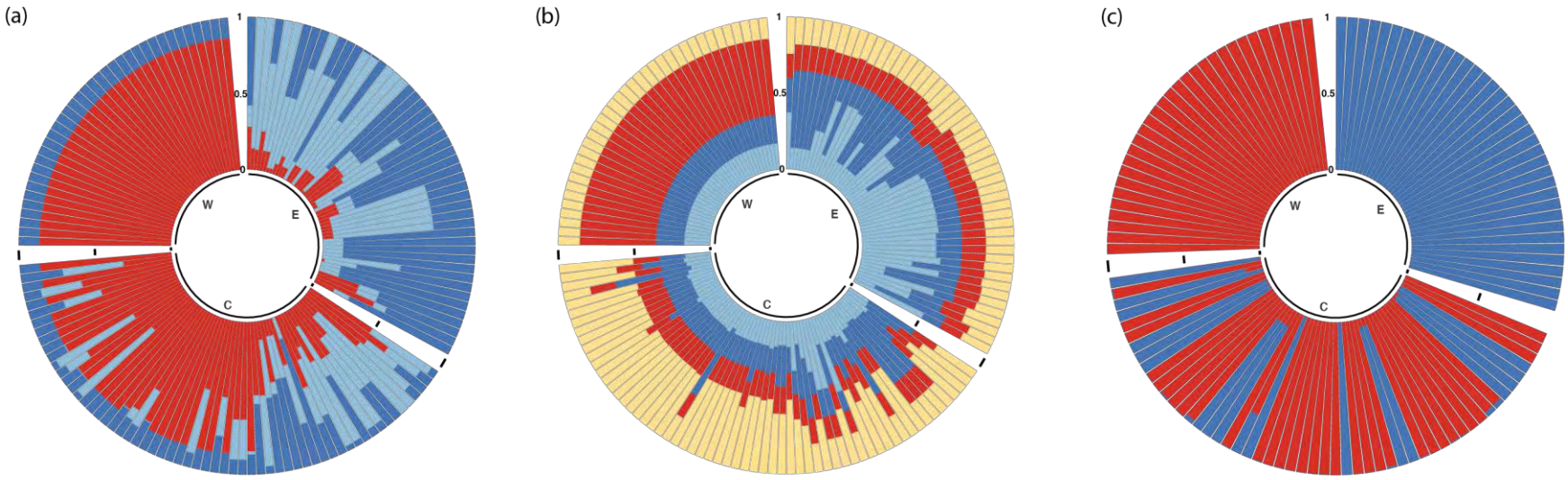


Figure S4. Cluster analyzes that show the phenetic relationships among shapes: (a) dorsal view, (b) braincase, (c) rostrum, (d) glenoid fossa, and (e) posterior edge of the palatine. The numbers indicate the bootstrap value.

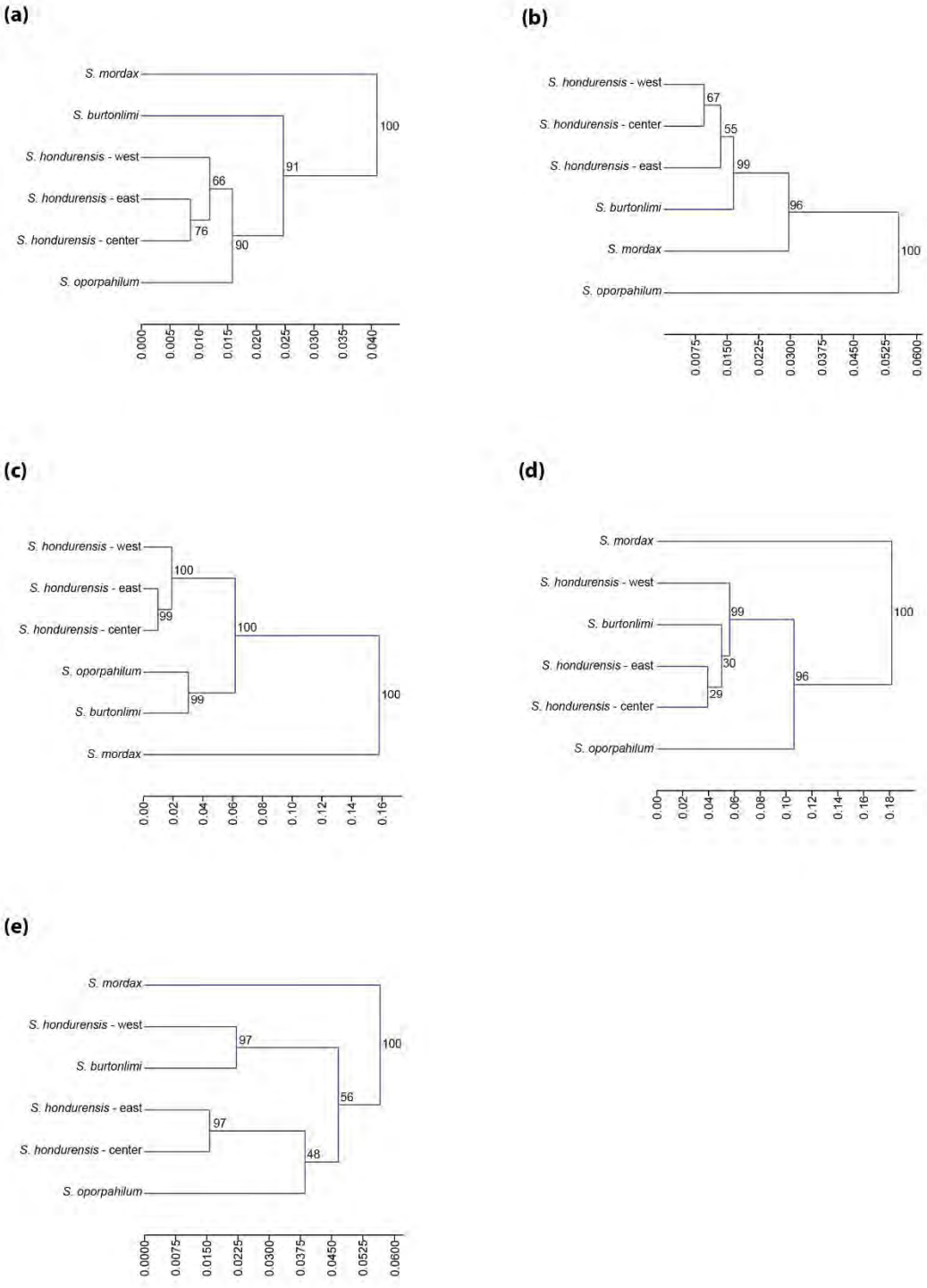


Figure S5. Means and standard error of centroid sizes: (a) dorsal view, (b) braincase, (c) rostrum, (d) glenoid fossa, and (e) posterior edge of the palatine. Blue = east, yellow = center, red = west.

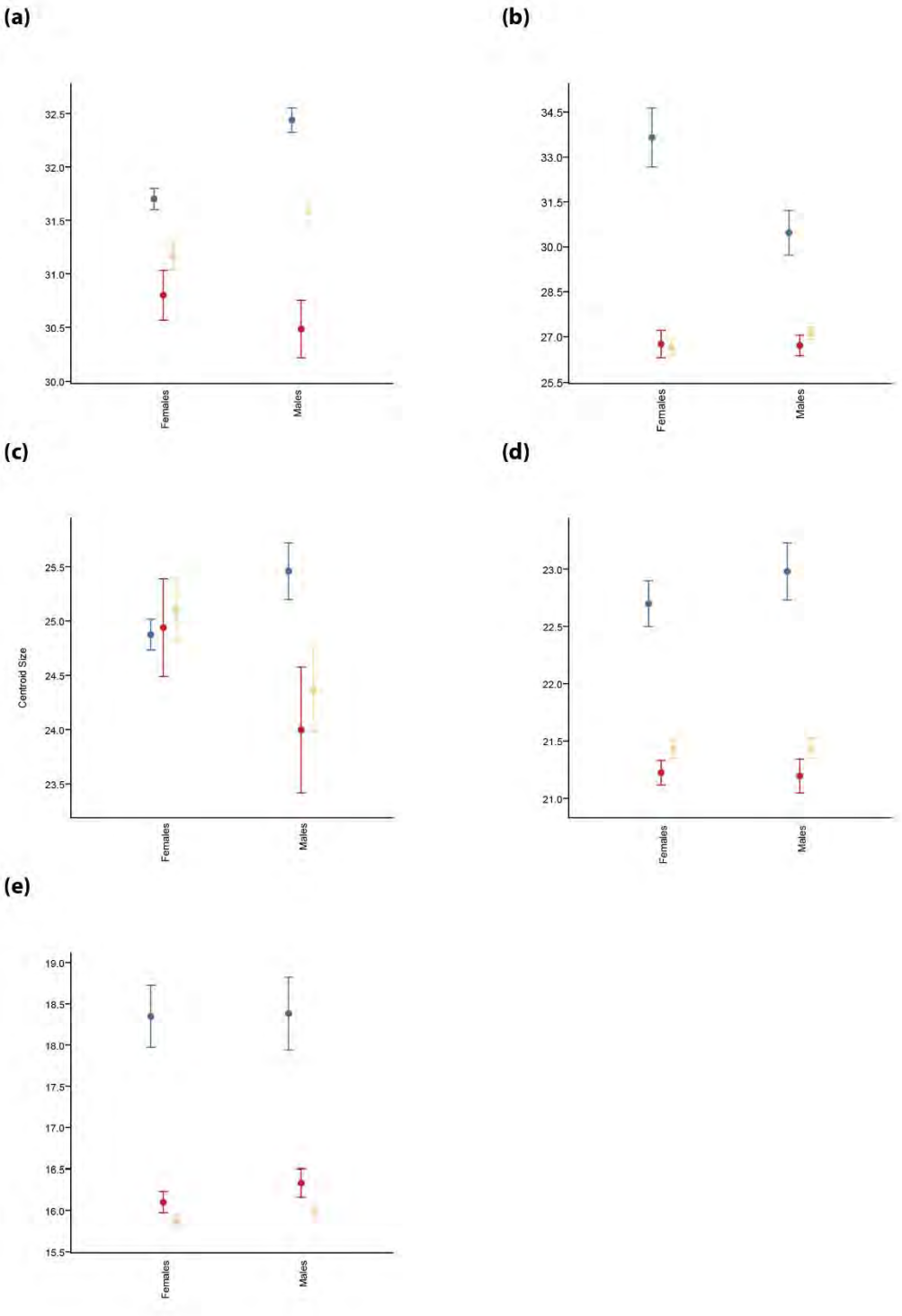


Figure S6. Scatter plots of CVAs and deformation grids of shape changes along the first canonical axis. (a) glenoid fossa – females, (b) glenoid fossa – males, (c) rostrum, (d) posterior edge of the palatine. In CVAs: blue = east, yellow = central, red = west groups. In deformation grids, the color represents the degree of variation in the shapes, red indicates expansion whereas blue contraction.

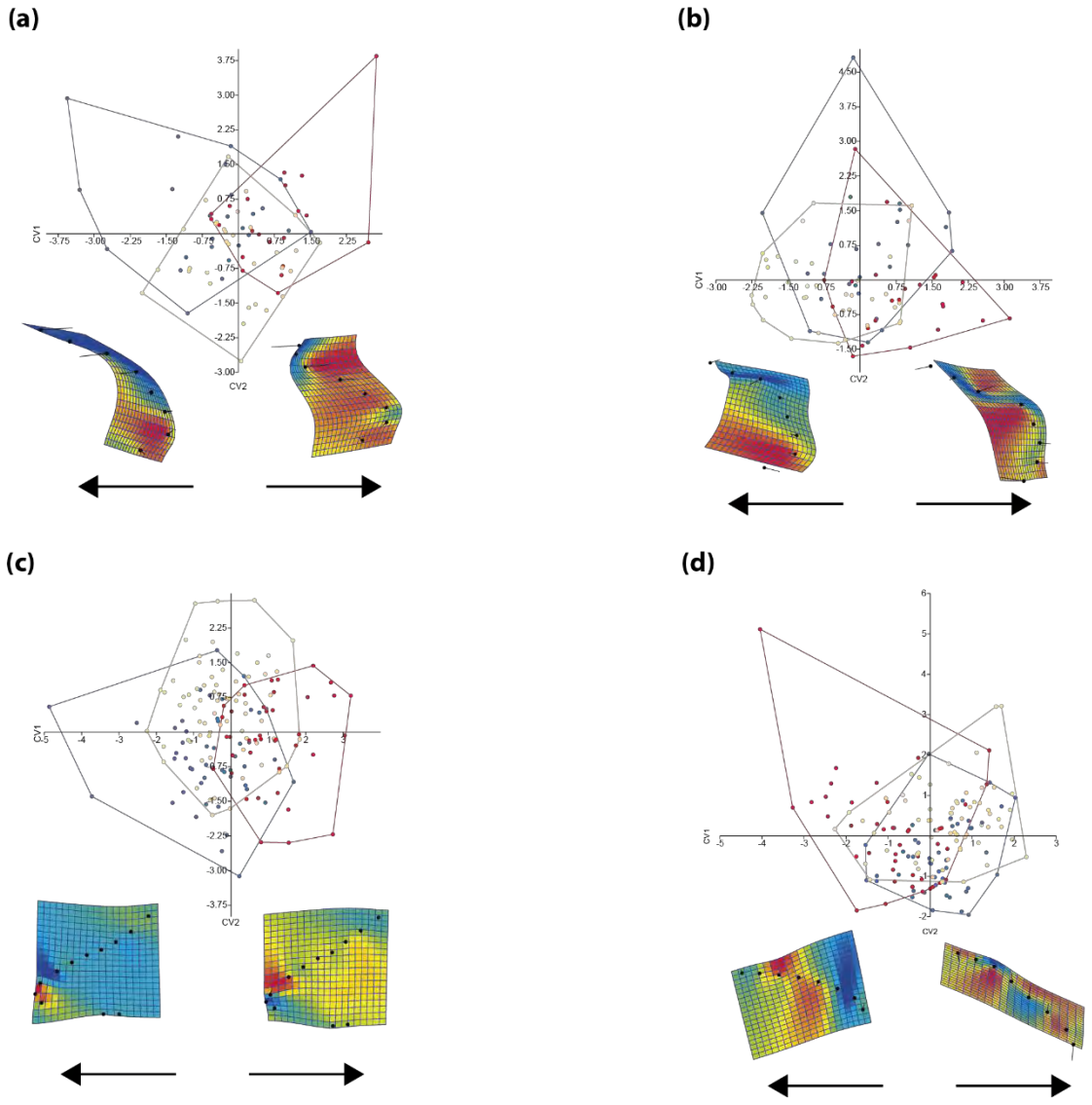


Figure S7. Means and standard error of measurements of the skulls: (a) length, and (b) width. Blue = east, yellow = center, red = west.

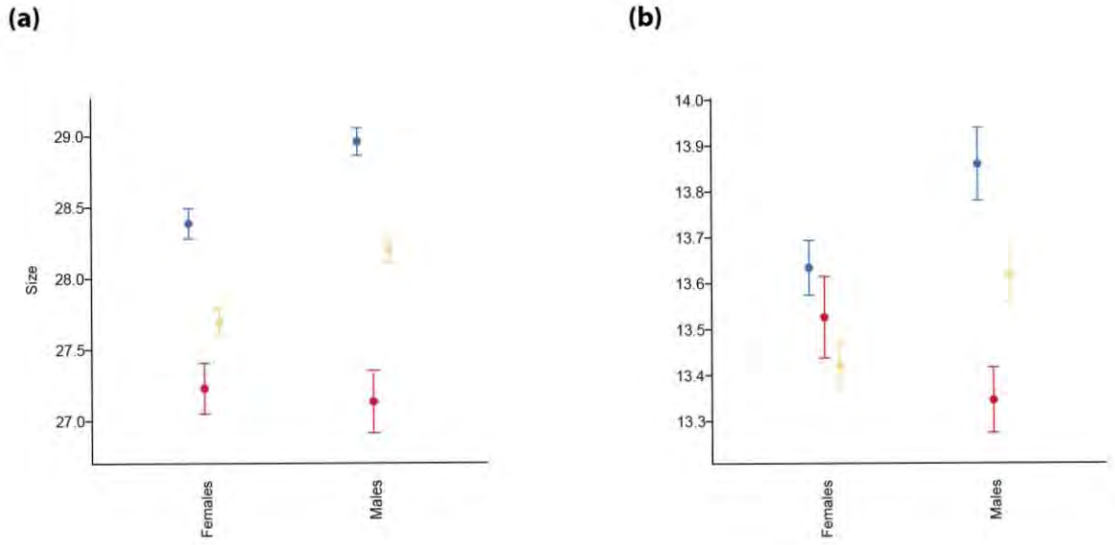
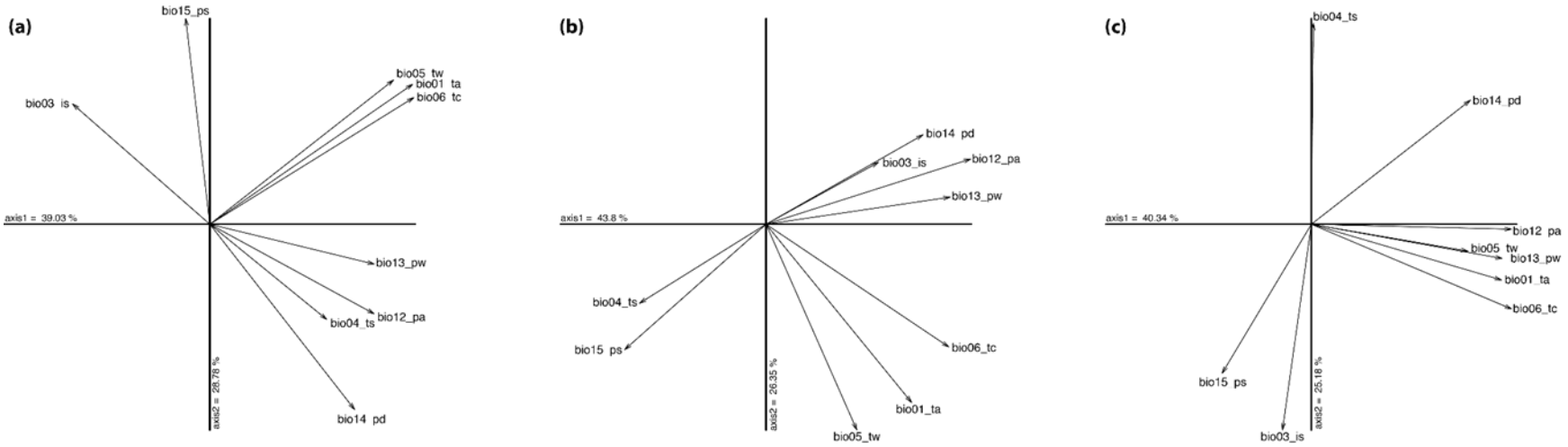


Figure S8. The contribution of the climatic variables on the two axes of the PCA and the percentage of inertia explained by the axes. The comparison are (a) Western vs Central, (b) Western vs Eastern; and (c) Central vs Eastern. Variables that characterize temperature were: annual mean (bio01_Ta), isothermality (bio03_Is), seasonality (bio04_Ts), maximum in the warmest month (bio05_Tw), and minimum in the coldest month (bio06_Tc); whereas variables that characterize precipitation were: total annual (bio12_Pa), total in wettest month (bio13_Pw), total in driest month (bio14_Pd), and seasonality (bio15_Ps).



CAPÍTULO 4.

Sturnira hondurensis (Chiroptera: Phyllostomidae)

En preparación: Mammalian Species

Giovani Hernández-Canchola, Jorge Ortega y Livia León-Paniagua

Resumen

El murciélago mesoamericano de tierras altas y hombros amarillos (*Sturnira hondurensis*, Goodwin, 1940) es un murciélago stenodermatino mediano, con un uropatagio vestigial, sin cola, y que generalmente presenta manchas rojizas o amarillentas en los hombros. Habita en regiones templadas desde México hasta el norte de Nicaragua, y es una de las 21 especies reconocidas y validadas en el género *Sturnira*. Es considerada una especie común, que no se encuentra en ninguna categoría de riesgo. Sin embargo, principalmente depende de la preservación de bosques continuos y conservados, por lo que la conexión entre parches de vegetación, aunado a la disponibilidad de alimentos en paisajes modificados son estrategias para la preservación de esta especie y los beneficios ecológicos que ofrece.

MAMMALIAN SPECIES XX(XXXX):00-00

Sturnira hondurensis (Chiroptera: Phyllostomidae)

GIOVANI HERNÁNDEZ-CANCHOLA, JORGE ORTEGA AND LIVIA LEÓN-PANIAGUA

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Abstract.—The highland yellow-shouldered Mesoamerican bat (*Sturnira hondurensis* Goodwin, 1940) is a relatively medium sized Stenodermatinae bat with a vestigial uropatagium, without tail, which usually has reddish or yellowish stains on the shoulders. It inhabits in temperate habitats from Northern Nicaragua to Mexico, and is 1 of 21 recognized and validated species in the genus *Sturnira*. It is considered a common species, which is not found in any risk category. Nevertheless, the species primarily depend on the preservation of conserved and continuous forest, so the connection among vegetation patches and the availability of food in modified landscapes are strategies for the preservation of this species, and the ecological benefits that it offers. DOI: _____.

Key words.—bat, frugivore, Highland yellow-shouldered Mesoamerican bat, Mexico and Central America

Synonymy completed _____

Sturnira hondurensis Goodwin, 1940

Highland yellow-shouldered Mesoamerican bat

Sturnira hondurensis Goodwin, 1940:1. Type locality "La Cruze Grande, near San Jose; elevation about 3000 feet; Department La Paz, Honduras" (See nomenclatural notes).

Sturnira ludovici: Hershkovitz, 1949:441. Name combination (See nomenclatural notes).

Sturnira oporaphilum: de la Torre, 1961:113. Name combination.

Sturnira ludovici occidentalis Jones and Phillips, 1964:477. Type locality "Plumosas, 2500 feet elevation, Sinaloa", Mexico (See nomenclatural notes).

Sturnira ludovici ludovici: Jones and Phillips, 1964:477. Name combination.

Sturnira ludovici hondurensis: Koopman, 1994:X. Name combination.

Sturnira hondurensis hondurensis: Ramírez-Pulido et al., 2014:13. First use of current name combination.

Sturnira hondurensis occidentalis: Ramírez-Pulido et al., 2014:13. First use of current name combination.

Sturnira hondurensis ludovici: Téllez-Girón, 2014:737. Name combination.

CONTEXT AND CONTENT. Order Chiroptera, family Phyllostomidae, subfamily Stenodermatinae, tribe Sturnirini, genus *Sturnira*. The genus *Sturnira* at least includes 21 recognized and validated species (Molinari et al. 2017): *Sturnira adrianae* Molinari et al., 2017; *Sturnira angeli* de la Torre, 1966; *Sturnira aratathomasi* Peterson and Tamsitt, 1968; *Sturnira bakeri* Velazco and Patterson, 2014; *Sturnira bidens* (Thomas, 1915); *Sturnira bogotensis* Shamel, 1927; *Sturnira burtonlimi* Velazco and Patterson, 2014; *Sturnira erythromos* (Tschudi, 1844); *Sturnira hondurensis* Goodwin, 1940; *Sturnira koopmanhilli* McCarthy et al., 2006; *Sturnira lilium* (É. Geoffroy Saint-Hilaire, 1810); *Sturnira ludovici*

Anthony, 1924; *Sturnira luisi* Davis, 1980; *Sturnira magna* de la Torre, 1966; *Sturnira mordax* (Goodwin, 1938); *Sturnira nana* Gardner and O'Neill, 1971; *Sturnira oporaphilum* (Tschudi, 1844); *Sturnira parvidens* Goldman, 1917; *Sturnira paulsoni* de la Torre and Schwartz, 1966; *Sturnira perla* Jarrín-V and Kunz, 2011; and *Sturnira tildae* de la Torre, 1959. Nevertheless, there are two more species in the genus *Sturnira* that need to be characterized genetically to determinate if they represent additional species, or are synonyms of recognized forms (Velazco y Patterson 2013): *Sturnira mistratensis* Contreras-Vega and Cadena, 2000; and *Sturnira sorianoi* Sánchez-Hernández et al., 2005. Besides, *Sturnira* new species 3 (*sensu* Velazco and Patterson 2013) represents another genetic lineage, that needs to be characterized morphologically and be described as a new species.

In *S. hondurensis* are recognized two subspecies: *Sturnira hondurensis hondurensis* Goodwin, 1940 and *Sturnira hondurensis occidentalis* Jones and Phillips, 1964 (Ramírez-Pulido et al. 2014). The subspecies *S. h. occidentalis* is smaller and paler than *S. h. hondurensis*, and also has a relatively broader skull with a shorter and abruptly elevated rostrum (Jones y Phillips 1964).

NOMENCLATURAL NOTES. The correct name of type locality is "La Cruz Grande", as is written in the original label of the type specimen. *Sturnira hondurensis* was described in 1940 by Goodwin as a smaller species with lower incisors deeply bilobed instead of simple, in contrast with *S. ludovici*. Nevertheless, *S. hondurensis* was synonymized to *S. ludovici* by Hershkovitz (1949) due to he noted that some Colombian *S. ludovici* with bilobate lower incisors wear these teeth and lost this characteristic with the age. Molecular and morphological reviews of genus *Sturnira* supported evidence to recognize *S. hondurensis* as an independent Mesoamerican species, close related to *S. burtonlimi* (found in Costa

Rica and Panama), *S. adrianae* (Venezuela and Colombia), *S. ludovici* (Colombia and Ecuador) and *S. oporaphilum* (Ecuador, Peru, Bolivia and Argentina—Iudica 2000; Velazco and Patterson 2013, 2014; Molinari et al. 2017).

Sturnira comes from the latin *sturnirus* or *sturnus* (starling), possibly in memory of the "H. M. S. Starling", an escort vessel on which the genera type was collected. The specific epithet *hondurensis* is in recognition of the type specimen being from Honduras (Gannon et al. 1989; Sánchez-Hernández et al. 2016).

DIAGNOSIS

Sturnira hondurensis has four lower incisors, whereas *S. bidens* and *S. nana* have only two functional inferior incisors (Molinari y Soriano 1987). Unlike some other species of this genus (*S. angeli*, *S. aratathomasi*, *S. bakeri*, *S. lilium*, *S. luisi*, *S.* new species 3, *S. parvidens*, *S. paulsoni*, *S. perla*, and *S. tildae*), in *S. hondurensis* the metaconoid and entoconoid in m1—2 are not separated by a deep notch (Iudica 2000). *Sturnira hondurensis* can be easily distinguished from *S. magna* by its smaller size (de la Torre 1966): forearms length of *S. hondurensis* = 38.58—46.9 mm, and in *S. magna* = 56.3—59.6 mm; greatest length of the skull of *S. hondurensis* = 21.7—25.6 mm and *S. magna* = 27.9—29.1 mm. Whereas the paladar of *S. hondurensis* is depressed, in *S. bogotensis* and *S. erythromos* is flat (Pacheco y Patterson 1991). In *S. hondurensis* all teeth are together, but in *S. koopmanhilli* there are diastemas among premolars and molars (McCarthy et al. 2006). The I1 in *S. hondurensis* have a single cusp, in contrast with the upper central incisors of *S. adrianae*, *S. ludovici*, *S. mordax* and *S. oporaphilum* that are bilobed (Velazco y Patterson 2014; Molinari et al. 2017). There is no a small distal cusp on P3 in *S. hondurensis*, whereas this cusp is present in *S. burtonlimi* and *S. oporaphilum* (Velazco y Patterson

2014). The direction of the premetacrista in M1 is oblique to the upper alveolar plane in *S. hondurensis*, but it is perpendicular in *S. burtonlimi*. Lower canines are not laterally divergent in *S. hondurensis*, but they are laterally divergent and shafts slanted outward in *S. burtonlimi* and *S. ludovici* (Velazco y Patterson 2014). The hypothetical *S. sorianoi* has lower incisive trilobed and in *S. hondurensis* are bilobed (Sánchez-Hernández et al. 2005).

GENERAL CHARACTERS

Sturnira hondurensis is a relatively medium sized stenodermatine bat with a simple face. The eyes are relatively large and eyelids have eyelashes. Ears are sharp-pointed, and tragus is long, falcate, curved, and tapering to a point. A large antitragus forms a thickened horizontal ledge at the base of the ear. Two glandular ridges originate lateral to the anterior base of the noseleaf and continue dorsally until the level of the eyes. The nares are directed anteriorly and are located in the basal part of the well-developed triangular noseleaf. The upper lip is simple and has small and variable warty growths. The lower lip has wart-like cutaneous pads: small pads forming a semicircular row surround a large central pad (Fig. 1—Goodwin 1940; de la Torre 1961; Sánchez-Hernández et al. 2016).

The propatagium originates medially at the level of the shoulder. The plagiopatagium extends laterally down to the ankles and is sparsely haired with short hairs. The IV metacarpal is shorter than the III one. The species has a vestigial uropatagium, and the trailing edge of the uropatagium is densely furred with long hairs (7.0—9.0 mm); there is no tail and the calcaneus is very low (de la Torre 1961; Velazco y Patterson 2014).

The color of the fur ranges from dark gray to dark brown, and the ventrum is paler. Youth are paler, and most individuals, especially adult males, have reddish or yellowish stains on the shoulders. Dorsal pelage between the shoulders is tetracolored and long (7.0—

10 mm), whereas ventrally the hairs are long (8.0 mm) but monocolored. The proximal portion of the forearm, the dorsal surfaces of the femur, tibia, feet and digits of the feet are densely covered with long hairs (Fig. 2—Téllez-Girón 2014; Velazco and Patterson 2014; Sánchez-Hernández et al. 2016).

The ranges of standard external measurements (in mm or g) in specimens of *S. h. occidentalis* from Colima, Jalisco and Sinaloa (Mexico–Jones and Phillips 1964; Sánchez-Hernández et al. 2002, 2016), followed by the ranges individuals of *S. h. hondurensis* from Eastern Mexico, Guatemala, El Salvador, Honduras and Nicaragua (Goodwin 1940; Lukens y Davis 1957; de la Torre 1961; Jones et al. 1971; Swanepoel y Genoways 1979; Velazco y Patterson 2014) are: head and body length = 52—77 / 65—77, hind foot length = 11—16 / 12—15, ear length = 12.0—19.0 / 12.9—19, forearm length = 38.58—44.93 / 43.0—46.9, and weight = 12.0—22.5 / 26.8.

Ranges of cranial measurements (in mm) of *S. h. occidentalis* and *S. h. hondurensis* (previously mentioned in addition with those from the Mexican states of Durango and Jalisco—Jones and Phillips 1964) are: greatest length of skull = 21.7—24.23 / 21.8—25.6, condyle-canine length = 19.0—20.79 / 20.1—22.2, zygomatic breadth = 12.49—14.3 / 12.5—14.2, mastoid breadth = 10.8—12.48 / 11.5—12.4, braincase breadth = 9.58—10.70 / 10.1—10.6, maxillary toothrow length = 5.8—7.36 / 6.3—7.2, mandibular toothrow length = 6.7—8.17 / 7.2—8.0, and interorbital width = 5.3—7.71 / 6.0—6.3 (Fig. 3). In *S. hondurensis* from Oaxaca, Mexico it was suggested that males average slightly larger than females (Swanepoel y Genoways 1979).

DISTRIBUTION

Sturnira hondurensis occidentalis is located in Western Mexico (from Southern Sinaloa and Durango to Jalisco—Jones and Phillips 1964). Sánchez-Hernández et al. (2002) suggested that *S. h. occidentalis* inhabits until the state of Colima (Mexico). On the other hand, *S. h. hondurensis* inhabits from Nuevo León and Tamaulipas in the Mexican Gulf Slope southward to Northern Nicaragua. The distribution of *S. h. hondurensis* includes the Trans Volcanic Belt and Sierra Madre del Sur, but it does not include Yucatan Peninsula (Fig. 4). *Sturnira hondurensis* has been found from sea level up to 2900 meters (Lavariega et al. 2012; Téllez-Girón 2014; Molinari et al. 2017). No fossils are known.

FORM AND FUNCTION

Form.—The skull of *Sturnira hondurensis* is relatively long and narrow, and the braincase moderately high with fairly well-developed sagittal crest (Goodwin 1940). The brain of *S. hondurensis* closely resemble to the one in *S. parvidens*. It has deep and extremely smooth cerebral hemispheres. The pseudocentral sulci and sulci anterior to the pseudocentral sulci are poorly developed, compared with other stenodermatine bats. The pseudotemporal lobes are angular and project ventrally. The inferior colliculi are completely covered, and the cerebellums is simple and has a medial crest (McDaniel 1973).

The rostrum is slender, the basisphenoid pits are deep divided by a high septum, the spenorbital fissure is subcircular, the anterior process of the glenoid fossa is well developed, the clinoid processes are absent, and the proximal end of the stylohyoid is narrow (Velazco y Patterson 2014). Phillips et al. (1977) described in detail the gross anatomy and histology of the parotid, submandibular and sublingual glands. In summary,

the parotid gland is extremely large and is posterior to the masseter, in the midline of the throat. It is a compound acinar gland that is densely packed with elongate secretory acini comprised of typical serous cells, and is characterized by an extensive system of ducts. Stenson's duct arises from the anterior edge of the parotid until the oral cavity at the level of the posterior side of the canines. The submandibular gland is large and triangular, which fills the cervical fossa. It is a compound tubuloacinar gland with large and densely packed secretory acini. The duct system of the submandibular is relatively simple, the Wharton's duct arises from the center of the inferior surfaces and is joined to the main duct from the sublingual gland, and together they opening near first lower premolar. The sublingual gland has a moderated size, which is triangular and soft. It is unilobular but its numerous fine subdivisions can be seen clearly. The sublingual is a compound tubuloacinar gland comprised of mucous cells with a duct system relatively simple.

Teeth of *S. hondurensis*, enamel provides the outer protective covering that surround the dentin, which is the major component of the teeth. The coronal portion of the dentin is characterized by distinct dentinal tubes (highly arborized) that follow a general S-shaped path from the pulpal chamber to the dentinoenamel junction. A moderate thickness layer cementum covers the roots, and it is the softest of the three types of hard dental tissue. The pulpal cavity is filled with a complex soft tissue that is continuous with the periapical tissue through the apical foramen of the roots. In *S. hondurensis*, the pulp most often is healthy and odontoblastic cells are essentially normal. Nonetheless, extensive hyperemia (dilation of capillaries) is commonly found in this species. This condition has been shown to be either transitory or an indication of early pulpitis (Phillips et al. 1977). Dental formula is i 2/2, c 1/1, p 2/2, m 3/3 total = 32 (Téllez-Girón 2014). I1 are unicuspidate and I2 are reduced (Jones y Phillips 1964). The direction of premetacrista in M1 is oblique to the

upper alveolar plane, and there is one labial cusp in M3 (Velazco y Patterson 2014). P3-4 and M1 are in straight slightly diverging lines, but M2-3 are at an angle directed inward. i1-2 are deeply bilobated, nevertheless these teeth wear with the age as in other member of the genus *Sturnira* (Goodwin 1940; Hershkovitz 1949). The lower canines are not laterally divergent (Velazco y Patterson 2014). In m1-2 the paraconid and metaconid are poorly defined, and the entoconid suppressed with no division between them and the metaconoid (Hershkovitz 1949).

Sturnira hondurensis has a simple stomach with a well-developed, elongate and tapers cardiac vestibule. The cardiac caecum is small, and the fundic caecum is saccular and thin-walled, which forms a spacious chamber with an apex. The pyloric valve is vestigial. The gastroesophageal junction lies well superior to the gastroduodenal junction, and the last one is clearly marked. The corpovestibular and vestibulocaecal junctions are marked by distinct sulci that anastomose near the midregion of the stomach. The tunica muscularis is bilaminate and the tunica submucosa forms the rugae, which in general are longitudinally oriented; there are numerous branches forming transverse secondary folds, but the elastic fibers are not many. In tunica mucosa, cardiac glands surround the gastroesophageal junction, and they are weakly reactive or non reactive to demonstrate the presence of acid mucopolysaccharides. Oxyntic glands occupy the cardiac vestibule, the cardiac caecum and a portion of the corpus. In the basal third of these glands, there are numerous alpha chief cells and few mucous gland cells. As oxyntic glands disappear, transitional glands (mainly mucous cell glands) become increasingly more apparent. There are cells within the bases of the pyloric glands, which are histologically identical to the submucosal glands of Brunner located in the uppermost duodenum (Rouk 1973; Forman et al. 1979). The description of the stomach of *S. hondurensis* resembles to the one in *S.*

parvidens, nonetheless, there are some differences between species. In *S. hondurensis* the stomach is more robust, the pyloric tube is shorter, the pyloric sphincter is only a short projection on the lesser curvature, the musculature of the terminal portion is relatively thinner, and mucous neck cells in the lower portion of the fundic glands are more abundant (Forman 1973). *S. hondurensis* has a mean gut area of 4.34 cm^2 (Saldaña-Vázquez et al. 2015).

The hair of *S. hondurensis* is bicolor without medulla, and the scales are coronal and unequal hastate (Baca-Ibarra y Sánchez-Cordero 2004). In Honduras, the stable hydrogen isotope ratios ($^2H/^1H$ or δD) in hair keratin was -96.2 % (± 10.0 SD) at 1,202 meter above sea level (m.a.s.l.) and -95.0 % (± 7.4 SD) at 1,546 m.a.s.l. (Erzberger et al. 2011). In Nicaragua, the δD in claws was -78.8 % and in hair was -80.7 % (Fraser et al. 2010). In Hidalgo (Mexico) one pregnant female of 16 individuals presented signals of leucism in both wings (García-Morales et al. 2012b). In the same Mexican state, another pregnant female with an embryo about to be born had a white spot over the left eye until the mouth (Sánchez-Hernández et al. 2012). In Oaxaca (Mexico) the wing aspect ratio of this species was 11.11, and the relative wing loading was 5.97 (García-García et al. 2014).

Function.— Based on seed defecated by *S. hondurensis* and *S. parvidens*, the similarity index of diet was 0.705 (García-Morales et al. 2012a), nevertheless, the digestive capacity of *S. hondurensis* was 0.46 and its Shannon index of diet diversity was 3.20, lower values than the reported in *S. parvidens* (its congeneric and in some places sympatric species—Saldaña-Vázquez et al. 2015). This lower digestive capacity is related with the alimentary requirements of *S. hondurensis*, due it needs a diet based on fruits with high

concentration of carbohydrates and proteins (*Solanum* and *Piper*), avoiding low-quality fruits (Saldaña-Vázquez y Schondube 2013).

In captivity, the species loss weight when it was only fed with *Solanum nigricum*, the experimental plant with the highest concentration of carbohydrates and proteins. On the other hand, other bats died when they were fed only of plants with lower concentration of carbohydrates and proteins (*Conostegia volcanis* and *Solanum aphyodendron*—Iñiguez-Dávalos 2005). *Sturnira hondurensis* needs to find different resources of nitrogen and carbohydrates to increase or complete its diet (Iñiguez-Dávalos 2005), due to this bat is unable to adjust its energy intake when food has low nutrient content (Saldaña-Vázquez y Schondube 2013). It is why *S. hondurensis* changes it food intakes and feeding behavior when its food has different percentages of nutrients (Saldaña-Vázquez y Schondube 2013). Additionally, there is a positive relation between the time inverted during the feeding and the energy obtained (Iñiguez-Dávalos 2005).

ONTOGENY AND REPRODUCTION

In Western Mexico the reproductive pattern of *Sturnira hondurensis* seems to coincide with the highest concentration of fruits that are consumed by these bats, mainly *Solanum nigricans*. This event occurs between May and July, when it has been reported the major concentrations of juveniles and individuals with signals of reproductive activity (Iñiguez-Dávalos 2005). Something similar was detected in Eastern Mexico, where was detected a reproductive pattern located at the end of winter and beginning of the spring (Cabrera-Garrido 2016).

Pregnant females were found during January-February (Mexico: Guerrero), March (El Salvador: Santa Ana; Mexico: Puebla), April (El Salvador: Santa Ana; Mexico: Jalisco), May (El Salvador: Santa Ana), June (El Salvador: Santa Ana; Mexico: Guerrero, Jalisco), July (El Salvador: Santa Ana; Mexico: Jalisco), August (El Salvador: Santa Ana; Mexico: Chiapas, Puebla), September-October (El Salvador: Santa Ana), November (Mexico: Jalisco), and December (Mexico: Guerrero). In all cases the females had a single embryo (Jones y Phillips 1964; Villa-R. 1966; Watkins et al. 1972; Hellebuyck et al. 1985; Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016). One juvenile was registered in August (Mexico: Colima), and sub-adults during August (Mexico: Colima) and December (Guatemala—de la Torre 1961; Sánchez-Hernández et al. 2002).

There are two axillary mammary glands (de la Torre 1961), and lactating females were reported during March (Mexico: Puebla), April (El Salvador: Santa Ana; Mexico: Colima, Guerrero, Jalisco), May-June (El Salvador: Santa Ana; Mexico: Jalisco), July (El Salvador: Santa Ana; Mexico: Colima, Guerrero, Jalisco), August (El Salvador: Santa Ana; Mexico: Colima, Jalisco, Puebla), September (El Salvador: Santa Ana; Mexico: Jalisco), October (Mexico: Jalisco, Puebla), November (El Salvador: Santa Ana), December (Guatemala—de la Torre 1961; Baker and Phillips 1965; Watkins et al. 1972; Hellebuyck et al. 1985; Sánchez-Hernández et al. 2002; Iñiguez-Dávalos 2005; Jímenez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016). Whereas post-lactating females were reported during April (El Salvador: Santa Ana; Mexico: Guerrero), May (El Salvador: Santa Ana), June (El Salvador: Santa Ana; Mexico: Guerrero, Jalisco), July (El Salvador:

Santa Ana; Mexico: Guerrero), August-September (El Salvador: Santa Ana—Iñiguez-Dávalos 2005; Jímenez-Salmerón 2008; Morales-Rivas 2016).

Males with scrotal testes were reported during January (Mexico: Colima, Guerrero), February (Mexico: Guerrero), March (Guatemala; Mexico: Puebla), April (Mexico: Guerrero, Jalisco), May-June (Mexico: Jalisco), July (Mexico: Guerrero), September (Mexico: Guerrero, Jalisco), October (El Salvador: Santa Ana), November (Mexico: Guerrero), and December (Mexico: Colima, Guerrero—de la Torre 1961; Villa-R. 1966; Sánchez-Hernández et al. 2002; Iñiguez-Dávalos 2005; Jímenez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016).

ECOLOGY

Population characteristics.—*Sturnira hondurensis* is a dominant species in tropical montane cloud forests and shade coffee plantations located in Mexico (Hernández-Montero et al. 2011; García-Estrada et al. 2012), whereas it is relatively rare in Nicaragua confined to highlands of the central North (Jones et al. 1971; Medina-Fitoria y Saldaña-Tapia 2012). *S. hondurensis* is very sensitive to habitat fragmentation (García-García et al. 2014; García-García y Santos-Moreno 2014). This species is more abundant in conserved and continues forests than in landscapes dominated by shade-coffee plantations, artificial ecosystems, or fragmented areas which these bats uses as stepping stones that connect forests (Saldaña-Vázquez et al. 2010, 2013; Castro-Luna y Galindo-González 2012; Ávila-Gómez et al. 2015). The abundance of the populations of *S. hondurensis* is positively related to the

densities of understory chiropterochoric plants (Saldaña-Vázquez et al. 2010; Castro-Luna y Galindo-González 2012).

Although in youth *S. hondurensis* was reported a sex ratio of 1:1 (Iñiguez-Dávalos 2005) is common to find more adult females (Saldaña-Vázquez et al. 2010), and it has been reported that adult males only represent 27 to 33 percent of the populations of this species (Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Morales-Rivas 2016). It was suggested that males of *S. hondurensis* decrease their populations, migrate during parts of the year, or use marginal habitats to avoid competitions with females to allow them forage in areas where the food is more abundant and ensure the reproductive success (Iñiguez-Dávalos 2005; Saldaña-Vázquez et al. 2010, 2013).

Space use.—It has been said that *S. hondurensis* seemingly prefers habitats at high elevations (Lukens y Davis 1957; Hellebuyck et al. 1985; Sánchez-Hernández et al. 2016), and this means that the species mainly inhabits in temperate forests. *S. hondurensis* inhabits in tropical montane cloud forests, pine-oak and coniferous forests, and temperate riparian vegetation. The species is also common on the margins or transition between temperate and tropical forests, and it has been collected on scrubs (Jones y Phillips 1964; Watkins et al. 1972; Cornejo-Latorre et al. 2011; Cortés-Delgado y Sosa 2014; Rodríguez-Macedo et al. 2014; Téllez-Girón 2014). *S. hondurensis* has been netted in very humid environments mostly bordered by dense vegetation, on streams, bodies of water, canyons, temperate human orchards and crops of coffee (Jones y Phillips 1964; Watkins et al. 1972; Cortés-Delgado y Sosa 2014; Téllez-Girón 2014; Sánchez-Hernández et al. 2016).

Its home range varies widely among individuals (mean = 56.7, from 3.93 to 311.30 ha). The mean distance (in m ± SE) from the daytime roost to the foraging area in coffee plantation was 822.71 ± 383.4 and in forest was 590.78 ± 161, whereas the maximum distance travelled (in m ± SE) in coffee plantation was 1466.73 ± 340 and in forest was 776.82 ± 141.4 (Cortés-Delgado y Sosa 2014). *Sturnira hondurensis* use to travel more in perturbed areas than in natural forests, because the strong relationship between the abundance of these bats and the understory food items (Saldaña-Vázquez et al. 2010; Cortés-Delgado y Sosa 2014). Actually, it was reported that this species is less prone to leave continuous forest patches (García-García et al. 2014), and it mainly forages in the understory and canopy of forests (Saldaña-Vázquez et al. 2010), in primary vegetation, secondary vegetation with different grades of regeneration, coffee plantations and complex agro-systems (Galindo-González 2004; García-Estrada et al. 2006; García-Morales et al. 2016).

Notwithstanding *S. hondurensis* is not known for extensive night movements (García-García et al. 2014), it forages during all night. In Veracruz (Mexico) the species left its roots approximately half an hour after sundown (Cortés-Delgado and Sosa 2014), and in Tamaulipas (Mexico) was reported that there is a high temporal overlapping (but not significant) during foraging with its congeneric *S. parvidens* (Arriaga-Flores et al. 2012). Nevertheless, the highest peaks of activity reported in *S. hondurensis* are two hours after sunset (El Salvador: Santa Ana—Morales-Rivas 2016), and between 21 to 23 hours (Mexico: Guerrero—Jímenez-Salmerón 2008). During a census over two years in Veracruz, from 36 captures only 1 specimen was recaptured at 580 meters of distance of the original place of capture (Estrada et al. 1993).

Despite the species is found all year, the abundance of *S. hondurensis* changes through the time. In Western Mexico is more abundant between May and July, when the major reproduction activity take place (Iñiguez-Dávalos 2005). In Eastern Mexico were reported different levels of abundance between dry and rainy seasons (Hidalgo and San Luis Potosí—García-Morales et al. 2014, 2016), and lower abundance values were detected in June and in September-December in Guerrero (Jímenez-Salmerón 2008). In Honduras, the isotopes in hair keratin did no differ between populations at 1,202 and 1,546 m.a.s.l., indicating that the altitudinal gradient may be too small and/or that variation in hair keratin isotopes is too large to unravel altitudinal movements of less than 400 meters (Erzberger et al. 2011)

Sturnira hondurensis mainly roosts in hollows located from 1.3 to 8 m of height inside old live trees. These trees have a height from 9 to 25 m and a diameter at breast height from 25 to 149.1 cm, and they are surrounded by a great density of large trees with a high number of hollows. In Veracruz *S. hondurensis* uses next trees as roosts: *Enterolobium cyclocarpum*, *Liquidambar styraciflua*, *Quercus sartorii* and *Trema micrantha*. Other trees that are use less frequent as roosts are *Alchornea latifolia*, *Anonna cherimola*, *Cinnamomum effusum*, *Ficus crocata*, *Inga jinicuil*, *Inga paterno*, *Inga* aff. *spurio* and *Schizolobium parahyba*. The majority of the roosts were located in shade coffee plantations and tropical montane cloud forest, but some of them in pasture (Cortés-Delgado y Sosa 2014). It seems that this species does not use caves as day roosts because the reports are near to caves, but not inside them. For example, two non-reproductive adult females were captured in front of an abandoned mine shaft 85 and 115 minutes after dusk (Divoll y Buck

2013), and some specimens were collected over the course of a stream in front of a cave (León-Paniagua y Romo-Vázquez 1993).

In Colima (Mexico) were compared the environmental characteristics where *S. hondurensis* inhabits, versus places where the species has not been found. In that Mexican state this bat is found in the areas with higher values of annual precipitation (1047.4 mm), precipitation in coldest quarter (42.2 mm), mean diurnal temperature range (13.6° C) and temperature annual range (19.6° C). These places also have the driest quarter (11.6 mm), and the wettest quarter (720 mm). Besides, these sites have lower values of annual mean temperature (23.4), isothermality (69.2%), maximum temperature in warmest month (32.5° C), lower mean temperature in coldest quarter (21.2° C), driest quarter (22.2° C), warmest quarter (25° C), wettest quarter (24.4° C) and minimum temperature in coldest month (12.9° C—Sánchez-Hernández et al. 2016). In Michoacán (Mexico) the ecological characterization of *S. hondurensis* shows that the species inhabits in temperate forest with temperatures of 14—20° C and levels of precipitation of 800—1200 mm (Wang et al. 2003).

***Diet.*—**In spite of *S. hondurensis* mainly feeds of fruit and infrutescences of plant associated with early stages of successional vegetation, the species has a relatively large diet niche (Hernández-Conrique et al. 1997; García-Estrada et al. 2012). *Sturnira hondurensis* mainly eats plants of the families Solanaceae and Piperaceae, and the principal plant species that consume are *Coussapoa purpusii*, *Ficus cotinifolia*, *Ficus* spp., *Hedyosmum mexicanum*, *Maclura tinctoria*, *Manilkara zapota*, *Saurauia madrensis*, *Solanum aligerum*, *Solanum aphyodendron*, *Solanum chrysotrichum*, *Solanum erianthun*, *Solanum nigricans*, *Solanum schlechtendalianum*, *Solanum* spp., *Peperomia* spp., *Physalis*

spp., *Piper auritum*, *Piper hispidum*, *Piper lapathifolium* and *Piper* spp. Other plant species, consumed less frequently by *Sturnira hondurensis* are *Cecropia obtusifolia*, *Conostegia volcanalis*, *Drymaria* spp., *Epiphyllum anguliguer*, *Ficus cookii*, *Ficus obtusifolia*, *Ficus padifolia*, *Ficus* spp., *Garcinia intermedia*, *Juanulloa mexicana*, *Lycianthes geminifolia*, *Markea* spp., *Miconia glaberrima*, *Muntingia calabura*, *Piper amalago*, *Piper pseudo-lindenii*, *Piper yzabalanum*, *Solanum acerifolium*, *Solanum diforum*, *Solanum diphyllum*, *Solanum rudepanum*, *Sideroxylon palmeri*, *Trema micrantha*, *Vismia mexicana*, and some insects in the Order Hymenopthera and Diptera (Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; García-Estrada et al. 2012; García-Morales et al. 2012a, 2016; Cortés-Delgado y Sosa 2014; Hernández-Montero et al. 2015; Morales-Rivas 2016; Herrera y López 2017). Besides, it has been reported pollen in the hair, excretes or in the stomach of this species (e.g. *Alnus* spp., *Chiranthodendron pentadactylon*, *Cordia gerascanthus*, *Operculina* spp., *Pinus* spp.—Jiménez-Salmerón 2008). This bat choses its food mainly by the odor, and other factors as the size, grouping and position of the fruits does not affect its choice (Iñiguez-Dávalos 2005).

Sturnira hondurensis has been maintained under captivity for experimental porpoises, and the maximum time in captivity reported has been 3 months. They were fed with banana, guava, mandarin orange, melon, papaya, watermelon, water, and some cases its diet was fortified with nutritional supplements (Iñiguez-Dávalos 2005; Saldaña-Vázquez y Schondube 2013). Other reports indicate that *S. hondurensis* also consumes of capuli cherries (*Prunus serotina*), peaches (*Prunus persica*), Mexican hawthorns (*Crataegus mexicana*), and some plant of the family Moraceae (*Trophis*—Sánchez-Hernández et al. 2016).

Plants of *Solanum nigricans* eaten by this species germinated 2 days before than plants that were not eaten, and in the case of *Solanum aphyodendron* just the seeds that were eaten by this bats germinated (Iñiguez-Dávalos 2005). *Sturnira hondurensis* is considered a legitimate disperser of plants of genus *Solanum* (Hernández-Montero et al. 2011), and the main disperser of plants in early stages of successional vegetation in natural and modified tropical montane cloud forests (Hernández-Montero et al. 2011; García-Estrada et al. 2012).

Diseases and parasites.— *Sturnira hondurensis* is ecto-parasitized by the bat flies (Diptera: Streblidae) *Aspidoptera delatorrei*, *Aspidoptera falcate*, *Megistopoda proxima*, *Megistopoda theodori*, *Metelasmus pseudopterus*, *Trichobius brennani* and *Trichobius joblingi* (Whitaker and Morales-Malacara 2005; Dick 2013; Tlapaya-Romero et al. 2015; Cuxim-Koyoc et al. 2016; Ramírez-Martínez et al. 2016). The bat fly *Paratrichobius longicrus* is considered an incidental record or consequence of contamination (Dick 2013), whereas *Paratrichobius sanchezi* is an accidental record (Colín-Martínez et al. 2018).

Sturnira hondurensis is also ecto-parasitized by the mites *Paralabidocarpus tonatiae* (Chirodiscidae), *Macronyssoides kochi*, *Parichoronyssus euthysternum* (Macronyssidae), *Eudusbabekia lepidoseta* (Myobiidae), *Chirnyssoides brasiliensis* (Sarcoptidae), *Periglischrus ojastii* (Spinturnicidae), *Microtrombicula sturnirae*, *Parasecia bulbocalcar* and *Parasecia soucouyanti* (Trombiculidae—Morales-Malacara 1998; Whitaker and Morales-Malacara 2005; Colín-Martínez et al. 2018). The mites *Macronyssoides kochi* (Macronyssidae), *Eudusbabekia viguerasi* (Myobiidae) and *Radfordiella desmodi* (Macronyssidae) were reported as ecto-parasites of *S. hondurensis*, nevertheless, the first two were considered as accidental registers, whereas the last one

must correspond to a mistake during field collection (Morales-Malacara 1998; Colín-Martínez et al. 2018).

In Mexico, *S. hondurensis* was registered as a host of *Trypanosoma cruzi* (Rengifo-Correa et al. 2017). Likewise, in Tabasco (Mexico), *S. hondurensis* was considered as an incidental host of *Leishmania (L.) mexicana* (Berzunza-Cruz et al. 2015), nevertheless, is possible that the specimen analyzed was miss identified due to this species has not been collected in that tropical Mexican state. In two specimens from Guatemala, there was no evidence of the bacteria *Bartonella* spp. (Bai et al. 2011).

In two *S. hondurensis* specimens from Guatemala, there was no evidence of influenza A virus (Tong et al. 2012). There was also no evidence of Coronaviruses in Chiapas (Mexico), in 7 and 16 specimens collected in undisturbed and disturbed areas (Anthony et al. 2013). In the same Mexican state there was no evidence of Venezuelan equine encephalitis virus, Eastern equine encephalitis virus, Western equine encephalitis virus, West Nile virus, and dengue virus in one specimen from an undisturbed area and another from a disturbed area (Sotomayor-Bonilla et al. 2014, 2017). In Mexican areas with concurrent dengue cases, *S. hondurensis* and other bats are not involved as reservoirs in dengue virus sylvatic cycle (Cabrera-Romo et al. 2016).

Interspecific interactions.—Due to the geographical distribution of *S. hondurensis*, this species could inhabits only with one member of the same genus: *S. parvidens*. *Sturnira hondurensis* is commonly found with other frugivorous or pollinivorous bats. It has been collected in the same nets with other bat species as *Anoura geoffroyi*, *Artibeus jamaicensis*, *Artibeus lituratus*, *Carollia perspicillata*, *Carollia sowelli*, *Centurio senex*, *Chiroderma*

salvini, *Dermanura azteca*, *Dermanura tolteca*, *Desmodus rotundus*, *Eptesicus fuscus*, *Glossophaga commissarisi*, *Glossophaga soricina*, *Hylonycteris underwoodii*, *Lasiurus borealis*, *Leptonycteris nivalis*, *Myotis keaysi*, *Myotis velifer*, *Pteronotus davyii*, *Pternotus parnellii*, *Rhogeessa gracilis* and *Tadarida brasiliensis* (Jones y Phillips 1964; Watkins et al. 1972; León-Paniagua y Romo-Vázquez 1993; Iñiguez-Dávalos 2005; Divoll y Buck 2013).

BEHAVIOUR

In experimental situation, *Sturnira hondurensis* was fed with *Solanum nigricans* and during 3 to 10 minutes it consumed the pulp, part of the shell and much of the seed; it defecated from 3 to 5 excretes with the 75 % of the seeds between 9 to 45 minutes after the fruit was ate. In the case of *Solanum aphyodendron*, the bats made an opening through they consumed the pulp and seeds from 2 to 5 minutes, and the bats defecated from 1 to 3 times including the 83 % of the seeds between after 5 to 23 minutes. Finally, in the case of *Conostegia volcanis*, *Sturnira hondurensis* only ate half of the fruit including the pulp, the shell and some seeds during 45 seconds to 3 minutes, it excreted between 2 to 4 times defecating around 500 seeds after 5 to 15 minutes (Iñiguez-Dávalos 2005).

GENETICS

The karyotype of *Sturnira hondurensis* (2n = 30, FN = 56) is identical to *S. parvidens* (Baker 1967; Hsu et al. 1968), and possibly identical to all other species inside

the genus *Sturnira* (Gannon et al. 1989). The X chromosome is a fairly large subtelocentric and the Y chromosome is a small submetacentric. Its autosomal chromosomes (in pairs) are: 7 metacentrics, 3 submetacentrics, and 4 subtelocentrics (Baker 1967). Through fluorescent in situ hybridization was detected that only two medium subtelocentric chromosomes possess ribosomal genes (rDNA—Baker et al. 1992).

There is a review of genus *Sturnira* based on partial mitochondrial cytochrome b gene and morphological data, which concluded that *S. hondurensis* is an independent species of *S. ludovici* (Iudica 2000). Additionally, sequences of the mitochondrial cytochrome c oxidase subunit 1 (COI) were used to analyze the geographically and genetically distinct groups within *S. ludovici* (*sensu latu*), and this research confirm that samples from El Salvador and Guatemala could represent a distinct and independent lineage of samples from Panama (Clare et al. 2011). Both previous results were reinforced by Velazco and Patterson (2013), based in the amplification of 3 mitochondrial (cytochrome b, hypervariable region HVRI section in Dloop, and ND2) and two nuclear (RAG1, and RAG2) loci. On the other hand, Iudica (2000) observed genetic variability in eastern population of *S. hondurensis*, and he suggested that these clades may represent undescribed species or subspecies.

Cross-species amplification in ten of twelve specifics microsatellite primers of *S. parvidens* were tested in three specimens of *S. hondurensis*. Five loci had not positive amplification, in other two the polymorphism was not probed because PCR conditions were not standardized, two had positive polymorphic amplification, and one had positive monomorphic amplification. Nevertheless, the success of these primers must be tested in more specimens (Gutiérrez et al. 2017).

CONSERVATION

In Veracruz was measured the bioaccumulation of persistent organochlorine compounds (OCPs) on riparian forests. The average concentrations of these pesticides (wet weight) in *S. hondurensis* were ΣDDT (p, p'-DDE, p, p'-DDD, p, p'-DDT) = 6.86 µg/g, ΣHCH (α, β, γ, δHCH) = 28.22 µg/g, Σheptachlor (heptachlor, heptachlor epoxide) = 2.62 µg/g, Σendosulfan (endosulfan I and II, endosulfan sulphate) = 4.60 µg/g, Σchlordane (metoxichlor, α chlordane) = 3.24 µg/g, and Σdrines (aldrin, dieldrin, endrin, aldehyde, endrin cetone) = 14.23 µg/g. Season or bat sex affects OCPs concentrations, and higher amounts of OCPs where found in transformed landscape than in forested landscape (Valdespino y Sosa 2017). Besides, the species is less abundant in modified and natural areas that use pesticides, herbicides and fertilizer (García-Estrada et al. 2006).

Sturnira hondurensis is considered a common species, which is not found in any risk category (Téllez-Girón 2014). Nevertheless, *S. hondurensis* is very sensitive to habitat fragmentation (García-García et al. 2014; García-García y Santos-Moreno 2014), and this species primarily depend of conserved and continues forest (Saldaña-Vázquez et al. 2010, 2013; Castro-Luna y Galindo-González 2012). To offer them constant resources in modified landscapes, farmers need to increase the size of native adjacent patches and allow the connectivity between vegetation fragments. Besides, farmers should allow the permanence of understory vegetation in their crops or in the surrounding. These management practices will allow a long-term survival of *S. hondurensis*, and must be considered in the restoration and management of transformed ecosystems, due to *S.*

hondurensis is important for regeneration of vegetation in conserved and modified landscapes (Iñiguez-Dávalos 2005; Saldaña-Vázquez et al. 2010, 2013; García-Estrada et al. 2012; García-Morales et al. 2012a; Cortés-Delgado y Sosa 2014).

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FIGURES

Fig.1.—An adult female of *Sturnira hondurensis* from Ahuatepec, municipality of Zongolica, Veracruz, Mexico. Photography taken in November, 2015. Used with permission of the photographer Alfredo Andrés Gutiérrez-González.

Fig.2.—An adult male of *Sturnira hondurensis* from Santuario de Bosque de Niebla, Área Natural Protegida Francisco Javier Clavijero, municipality of Xalapa, Veracruz Llave, Mexico. Photography taken in February, 2007. Used with permission of the photographer Antonio Guillén Servent.

Fig.3.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male of *Sturnira hondurensis* (MZFC-M [Museo de Zoología, Facultad de Ciencias – UNAM] 10015) from 1.3 km al NNW de Chiquihuites, municipality Unión Juárez, Chiapas, Mexico. Greatest length of skull, excluding incisor is 23.67 mm. Used with permission of the photographer Sara Carolina Lucero-Verdugo.

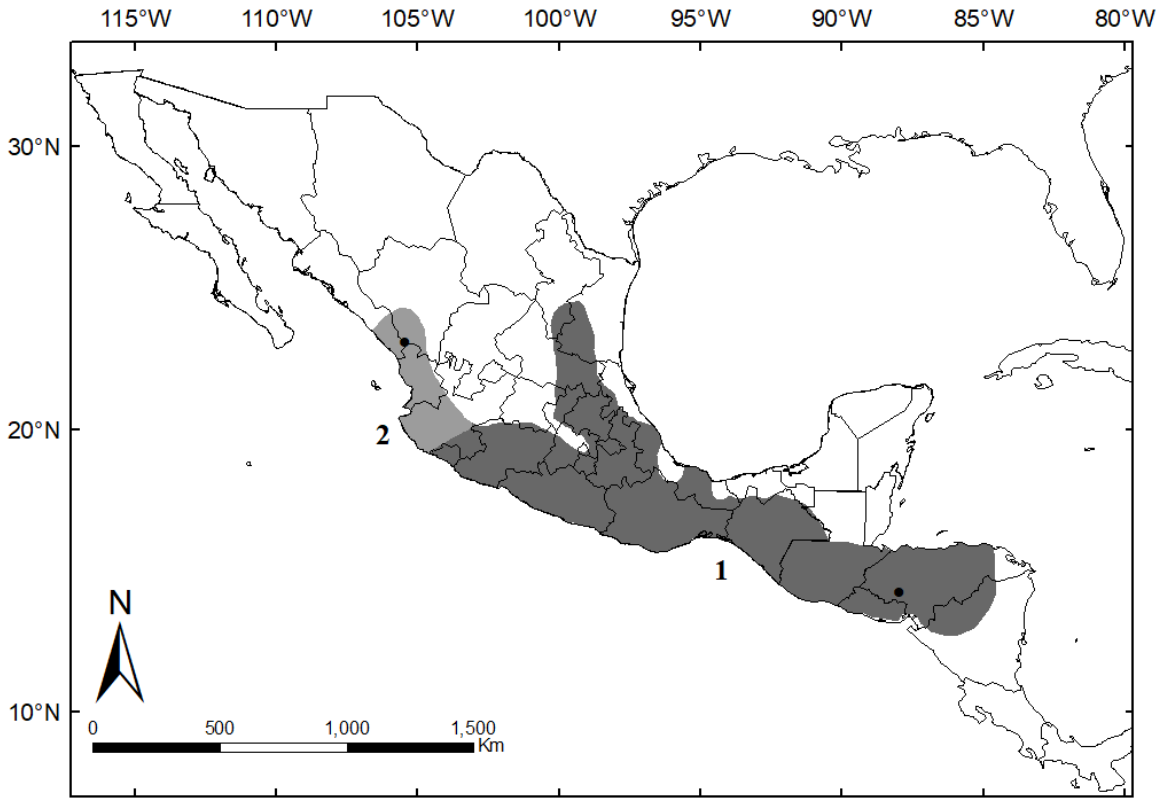

Fig.4.—Geographic distribution of *Sturnira hondurensis*. The subspecies are 1: *S. h. hondurensis*, and 2: *S. h. occidentalis*, according to Jones and Phillips (1964). The black dots show the type locality of each subspecies.

DISCUSIÓN GENERAL

La compleja geología mesoamericana, su historia biogeográfica, la gran diversidad de hábitats, climas, tipos de suelo y vegetación, así como los cambios climáticos que ocurrieron en el pasado ofrecen un valioso campo de estudio para investigar los procesos ecológicos y evolutivos de la región (Becerra y Venable, 2008; Gutiérrez-García y Vázquez-Domínguez, 2012). En este sentido, los análisis filogeográficos en combinación con el modelamiento de nicho ecológico son de gran utilidad para ayudar a comprender los complejos patrones y la historia evolutiva de su biodiversidad (Gutiérrez-Rodríguez et al., 2011; Hasbún et al., 2005).

Incongruencias y patrones filogeográficos detectados

La comparación de la divergencia genética, espacial y temporal, el nivel de flujo genético y las dinámicas poblaciones entre varias especies codistribuidas generan información sobre los patrones filogeográficos existentes, que son la base para la inferencia histórica (Bagley y Johnson, 2014). De esta forma, los procesos evolutivos comunes, pero también sus desviaciones, incrementan nuestro entendimiento sobre el ensamble de comunidades y los procesos evolutivos (Shaw y Gillespie, 2016). Además, los procesos biológicos actuales también participan en estos mecanismos, ya que las diferencias ecológicas determinan la inclinación o las tasas de dispersión para establecerse en nuevas áreas (Bagley y Johnson, 2014). En este sentido, los estudios comparativos resultan ser métodos poderosos para identificar los factores que han influenciado la historia de la biodiversidad (Bagley y Johnson, 2014; Hodel et al., 2016). Sin embargo, cuando en estos análisis solo se

consideran especies de tierras bajas o de áreas montañosas, se obtiene una visión parcial acerca de los procesos de diversificación. Estudiar diferentes tipos de especies puede darnos una imagen más completa sobre los diferentes procesos históricos y evolutivos que subyacen en una región (Brumfield y Edwards, 2007).

En este trabajo se observó cierta congruencia genética entre las dos especies estudiadas, ya que en ambas se detectó que el oeste de México actúa como una región que promueve la diferenciación de linajes. Sin embargo, los procesos evolutivos detectados entre especies son contrastantes y se relacionan con dos diferentes mecanismos que promovieron la diferenciación genética. Por una parte, en la especie asociada con hábitats montañosos–*S. hondurensis*– se observó que las características topográficas de la región en combinación con la historia climática son determinantes en sus procesos evolutivos. Como en otros taxones montanos con limitada capacidad de dispersión, la discontinuidad del paisaje es un factor muy importante, que restringe la dispersión e influye en la estructuración poblacional (Caviedes-Solis y Leaché, 2018). Por otra parte, en la especie tropical de tierras bajas –*S. parvidens*– la diferenciación intraespecífica fue posible aún en ausencia de barreras geográficas evidentes. En este caso, se ha sugerido que algunos eventos históricos fueron severos y promovieron la diferenciación genética entre linajes, la cual ha sido mantenida por factores ecológicos o conductuales (Avise, 2000; Jaramillo-Correa et al., 2008).

También existió cierto grado de congruencia demográfica, ya que las poblaciones del oeste de México mostraron tamaños poblaciones históricos más estables. Este patrón puede ser consecuencia de la topografía excepcionalmente rugosa del oeste de México que ha promovido la especiación alopátrica por medio de vicarianza (Becerra y Venable, 2008),

y que pudo mantener poblaciones aisladas en un área más estable durante los pasados cambios climáticos.

Sin embargo, no encontramos una congruencia temporal entre los procesos evolutivos de *S. hondurensis* y *S. parvidens*. Dado que habitan en ambientes contrastantes, es posible que las oscilaciones climáticas del Cuaternario hayan actuado de manera diferencial en cada especie. Mientras los periodos glaciales posiblemente promovieron la estructuración genética en *S. parvidens*, en *S. hondurensis* intensificaron el flujo genético entre poblaciones previamente aisladas, y el efecto contrario debió ocurrir durante los periodos interglaciales (Ramírez-Barahona y Eguiarte, 2013; Zarza et al., 2008). Para reforzar la hipótesis de que los patrones climáticos promovieron la divergencia de poblaciones por aislamiento geográfico, se podrían realizar proyecciones de distribuciones potenciales al pasado (Guevara et al., 2018).

Lo anterior sugiere que los procesos que afectaron a estas especies suelen ser especie-específicos, en los cuales la biología de las especies es determinante en los mecanismos de evolución biológica (Caviedes-Solis y Leaché, 2018; Velazco y Patterson, 2008). También destaca el oeste de México, un área que ha actuado como un centro de diversificación y diferenciación en múltiples ocasiones y en diversos taxones, debido a su compleja geología, historia climática y particularidades ecológicas (Arbeláez-Cortés et al., 2014; Hernández-Canchola y León-Paniagua, 2017). Esto es muy relevante para los mamíferos mexicanos, ya que esta región alberga a los géneros endémicos *Megasorex* (musaraña), *Musonycteris* (murciélago), *Hodomys*, *Nelsonia*, *Osgoodomys*, *Papogeomys*, *Xenomys*, y *Zygogeomys* (roedores), así como diversas especies endémicas de murciélagos y roedores (Ceballos, 2014). En esta región también se han reportado procesos de

diferenciación biológica en especies de peces, ranas, serpientes, iguanas, hormigas, árboles y aves, evidencia que señala una constante y activa diversificación de linajes en la región (Arbeláez-Cortés et al., 2014, y referencias en el mismo).

Es importante poner a prueba diferentes hipótesis estadísticas cuando se realizan comparaciones de los procesos evolutivos, ya que en múltiples programas de genética de poblaciones se considera un único escenario evolutivo bajo el cual diversos índices y valores son calculados, y raramente la historia evolutiva de todas las poblaciones se ajusta a estos modelos (Cornuet et al., 2008). Por ejemplo, el algoritmo DIYABC2 (Cornuet et al., 2014) es un método computacional de aproximación Bayesiano que utiliza parámetros definidos *a priori* y simulaciones basadas en coalescencia para generar sets de datos con el mismo número de copias de genes y *loci* como en los datos observados. En cada set simulado el programa estima diversos estadísticos de resumen que son comparados con los obtenidos en los datos observados, y finalmente se elige el mejor modelo al cual se ajustan los datos (Cornuet et al., 2008; Ramírez-Barahona y Eguiarte, 2014). De esta forma se podría determinar si los tamaños poblaciones de las dos especies mexicanas *Sturnira* han permanecido más estables en el oeste del país, y si dicha estabilidad ha sido constante a lo largo de múltiples cambios climáticos que siguieron después de la diferenciación de estas poblaciones.

Por otra parte, se puede observar incongruencias entre los tiempos de divergencia de poblaciones que habitan en una misma área geográfica, aun cuando son consecuencia del mismo evento vicariante. Esto puede deberse a la varianza del proceso coalescente relacionado con la demografía de cada especie (Ornelas et al., 2013). Para confirmar si los eventos de diferenciación intraespecíficos en las especies mesoamericanas del género

Sturnira ocurrieron en momentos independientes, se sugiere utilizar análisis que pongan a prueba la hipótesis de diversificación simultánea. Este estudio se podría realizar con el método Hierarchical Approximate Bayesian Computation, el cual utiliza métodos computacionales de aproximación Bayesiana bajo un modelo coalescente jerárquico que analiza la divergencia simultánea en múltiples pares de poblaciones codistribuidas. Para ello se estiman hiper-parámetros que caracterizar el grado variabilidad en los tiempos de divergencia entre pares de poblaciones co-distribuidas, permitiendo la variación en diversos parámetros demográficos dentro de pares de poblaciones (sub-parámetros) que pueden afectar la coalescencia (Hickerson et al., 2007). Estos resultados ayudarían a explorar formalmente si en Mesoamérica los procesos de diferenciación reciente fueron promovidos por la complejidad topográfica, por el efecto de las oscilaciones climáticas del Pleistoceno y/o por los procesos de especiación ecológica.

Es importante considerar que para obtener resultados con un buen soporte estadístico en ocasiones es importante incrementar el número de *loci* analizados, mientras que en otros casos resulta más conveniente incrementar el tamaño de la muestra (Streicher et al., 2016). Los datos genómicos generalmente brindan mayor información sobre el proceso evolutivo (Sturge et al., 2016), sin embargo, no siempre es necesario secuenciar el genoma completo de los organismos, debido a que existe un límite en el número de marcadores genéticos utilizados, después del cual la información obtenida será la misma (Weinman et al., 2015). Por otra parte, con la teoría coalescente se ha demostrado que aumentar el tamaño de muestra no necesariamente mejora las estimaciones de los procesos evolutivos (Salas-Lizana, 2013). Considerando que el par de análisis propuestos utilizan simulaciones coalescentes (DIYABC2 y Hierarchical Approximate Bayesian

Computation), se recomienda incrementar como prioridad el número de *loci* en lugar de incrementar el tamaño de muestra, ya que contamos con una adecuada representación geográfica de la distribución completa de ambas especies. Cabe señalar que con este objetivo en mente fueron diseñados primers de microsatélites, con los cuales se obtendrá más información molecular sobre los procesos evolutivos del género *Sturnira* (Anexo). Con esta información se podría evaluar de manera adecuada la relevancia del oeste de México en los procesos de diversificación reciente.

Implicaciones para la conservación

Las especies mesoamericanas de *Sturnira* fueron reconocidas recientemente como linajes independientes gracias a los estudios moleculares (Iudica, 2000; Velazco y Patterson, 2013), por lo que los análisis genéticos son de particular relevancia en este género, donde existen muchas especies crípticas que oscurecen la gran diversidad de especies existentes (Iudica, 2000; Pacheco y Patterson, 1991). La información generada y compilada en esta tesis aporta información relevante para comprender y proteger de manera adecuada la diversidad de un grupo de organismos que desempeñan papeles ecológicos muy importantes en los procesos de restauración ecológica (Cortés-Delgado y Sosa, 2014; Galindo-González et al., 2000; Hernández-Montero et al., 2015; Olea-Wagner et al., 2007), y de los cuales no existía conocimiento acerca de su diversidad genética.

Dentro de *S. hondurensis* y *S. parvidens* fueron detectados diversos linajes intraespecíficos, los cuales muestran señales de diferenciación ecológica. Si bien la evidencia señala que representan estadios tempranos en el proceso de formación de nuevas

especies, estos grupos ya muestran señales de adaptaciones ambientales a los medios en los que habitan. Con el objetivo de garantizar la viabilidad a largo plazo de los sistemas naturales, debe mantenerse su diversidad genética dentro y entre poblaciones, mantener sus patrones históricos de evolución independiente, además del potencial evolutivo entre las poblaciones de ambas especies (Vázquez-Domínguez y Vega, 2006). Por otra parte destacan los linajes del oeste mexicano, ya que resultan ser los más diferenciados, además de contar con distribuciones restringidas y endémicas a México. Es por ello que también debe considerarse su preservación, ya que se localizan en áreas prioritarias para la conservación de especies endémicas de mamíferos, pero en donde aún hacen falta muchos esfuerzos para lograrlo (Ceballos et al., 1998).

Si bien este par de murciélagos no se encuentran en ninguna categoría de riesgo y son considerados abundantes (Téllez-Girón, 2014; Téllez-Girón y Amin, 2014), su preservación resulta fundamental para mantener los ecosistemas y las funciones ecológicas de las regiones en las que habitan, ya que ambas son consideradas como unas de las principales especies dispersoras de semillas de plantas pioneras en ambientes perturbados y en estadios de sucesión temprana (e. g., García-Estrada et al., 2012; Hernández-Montero et al., 2011). A pesar de que estas especies se alimentan en ambientes abiertos y perturbados, sus sitos de percha se localizan principalmente en bosques y selvas muy conservados (Cortés-Delgado y Sosa, 2014; Fenton et al., 2000; García-Morales et al., 2014; Saldaña-Vázquez et al., 2010), por lo que algunas estrategias para su conservación son la conexión entre parches de bosques y selvas, además de promover la disponibilidad de alimento en los ambientes modificados, para asegurar que estas especies sigan promoviendo los procesos

de sucesión ecológica en paisajes modificados y/o perturbados (Evelyn y Stiles, 2003; Saldaña-Vázquez et al., 2010).

Los mecanismos de estructuración y flujo genético que sufrieron este par de especies también pueden ser muy interesantes y relevantes en el escenario del cambio climático global. *Sturnira hondurensis* y *S. parvidens* fueron especies afectadas por los últimos ciclos glaciales e interglaciales, los cuales presentan características muy semejantes al ciclo climático actual, mostrando una clara relación entre los gases de efecto invernadero (CO_2, CH_4) y el clima (EPICA, 2004). Sin embargo sólo los eventos más severos afectaron sus niveles de estructuración y diversidad genética, es decir son especies tolerantes a ciertos cambios climáticos globales. Es por ello que podrían ser candidatos ideales para enfrentar los estragos producidos por la pérdida de la vegetación y del cambio climático global. Para corroborar lo anterior, se recomienda el uso de marcadores moleculares que brinden información en una temporalidad actual. Por ejemplo, con el uso de los marcadores microsatélites se podría determinar el impacto de algunas actividades humanas, como la deforestación y la pérdida de hábitat, sobre los niveles de estructuración y diversidad genética (Castañeda-Rico et al., 2011). De esta manera se evaluaría con mayor robustez la relevancia de este par de especies para la continuidad de las funciones ecosistémicas en las regiones que habitan.

CONCLUSIONES

En este trabajo se analizó la filogeografía y los requerimientos climáticos de dos especies mesoamericanas del género *Sturnira*. A pesar de que los taxones analizados habitan en ecosistemas contrastantes, se detectaron diversas similitudes en los procesos evolutivos que han moldeado sus patrones de variación genética, como la formación de linajes intraespecíficos recientes con similitudes ecológicas y demográficas. Esta información destaca al oeste de México como una región importante para la diversificación de especies. Sin embargo, también se encontraron diferencias en los mecanismos evolutivos, relacionadas con las características particulares de cada especie. Posteriormente, se revisó que este par de especies son fundamentales en los procesos de sucesión ecológica y restauración de la cobertura vegetal. Si bien estas especies son abundantes, su preservación resulta importante para la continuidad de las funciones ecológicas que desempeñan y para la protección de sus linajes genéticos con distribuciones restringidas, los cuales presentan adaptaciones ambientales a los medios en los que habitan.

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ANEXO.

Isolation and characterization of microsatellite markers for *Sturnira parvidens* and cross-species amplification in *Sturnira* species

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Resumen

El género *Sturnira* se localiza desde México y las Antillas menores hasta Argentina, y es uno más ricos en número de especies en el Neotrópico. Este género forma un clado monofilético bien soportado con al menos 21 especies reconocidas, así como algunas otras bajo revisión taxonómica. *Sturnira parvidens* es un murciélago frugívoro de las selvas neotropicales que tiene una amplia distribución, es muy abundante y es un componente importante en la dispersión de frutos para la regeneración de ecosistemas. Utilizamos una técnica de secuenciación Ilumina para construir una librería enriquecida de *loci* de microsatélites para *S. parvidens*. Analizamos millones de resultados con un software especializado para extraer las lecturas que contenían microsatélites di-, tri-, tetra-, penta-, y hexanucleótidos. Seleccionamos y probamos 14 microsatélites polimórficos (di, tri, tetra). Todos ellos fueron genotipificados en 26 individuos de distintas localidades. Observamos una variación genética mediana y alta entre *loci*, pero solo 12 de ellos fueron funcionalmente polimórficos. Los niveles de heterocigocidad de todos los marcadores fue de alta a media (H_E promedio = 0.79, H_O promedio = 0.72). Examinamos la amplificación cruzada en 12 especímenes del género, obteniendo amplificaciones nulas, monomórficas y

polimórficas. Con este método fuimos capaces de identificar un número masivo de *loci* de microsatélites en poco tiempo, reduciendo costos comparados con otras técnicas, y obteniendo una gran cantidad de datos. Los *loci* polimórficos descritos para *S. parvidens* y para el género, podrán ser útiles en futuros análisis de genética con los cuales se podrían resolver inconsistencias taxonómicas, realizar análisis de parentesco, o evaluaciones de genética de poblaciones.

Isolation and characterization of microsatellite markers for *Sturnira parvidens* and cross-species amplification in *Sturnira* species

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ABSTRACT

Background. *Sturnira* is one of the most species-rich genera in the Neotropics, and it is found from Mexico and the Lesser Antilles to Argentina. This genus forms a well-supported monophyletic clade with at least twenty-one recognized species, as well as several others under taxonomic review. *Sturnira parvidens* is a widespread frugivorous bat of the deciduous forests of the Neotropics, is highly abundant, and is a major component in fruit dispersal to regenerate ecosystems.

Methods. We used a technique based on Illumina paired-end sequencing of a library highly enriched for microsatellite repeats to develop loci for *S. parvidens*. We analyzed millions of resulting reads with specialized software to extract those reads that contained di-, tri-, tetra-, penta-, and hexanucleotide microsatellites.

Results. We selected and tested 14 polymorphic (di, tri, and tetra) microsatellites. All markers were genotyped on 26 different individuals from distinct locations of the distributional area of *S. parvidens*. We observed medium—high genetic variation across most loci, but only 12 were functionally polymorphic. Levels of expected heterozygosity across all markers were high to medium (mean $H_E = 0.79$, mean $H_O = 0.72$). We examined ascertainment bias in twelve bats of the genus, obtaining null/monomorphic/polymorphic amplifications.

Discussion. The Illumina paired-end sequencing system is capable of identifying massive numbers of microsatellite loci, while expending little time, reducing costs, and providing a large amount of data. The described polymorphic loci for *S. parvidens* in particular, and for the genus in general, could be suitable for further genetic analysis, including taxonomic inconsistencies, parentage/relatedness analysis, and population genetics assessments.

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INTRODUCTION

The yellow-shouldered Mesoamerican bat (*Sturnira parvidens*) is primarily associated with lower elevations (0 to 2,000 m), and is found mainly in tropical/subtropical habitats and ecotones (*Villalobos & Valerio, 2002*). *S. parvidens* is found from the northern Mexican

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Pacific Slope and the northern Mexican Gulf Slope southward to Northern Costa Rica, and including the Yucatan Peninsula (G Hernández-Canchola & L León-Paniagua, 2017, unpublished data). *S. parvidens* has been caught in the understory and subcanopy of tropical and subtropical forests, in xeric scrubs, and in secondary and temperate forests. They are commonly found roosting in the foliage of forests of advanced successional stages, but their home ranges include mature and secondary forest (*Evelyn & Stiles, 2003*). They mainly consume fruit from plants representing early stages of plant succession, like pioneer trees (*Cecropia peltata*), pioneer herbs (*Solanum americanum*, *S. torvun*, *S. ochraceo-ferrugineum*, *Capsicum annuum*), or pioneer shrubs (*Piper hispidum*, *P. lapathifolium*; *Olea-Wagner et al., 2007*). This frugivorous species is an important seed disperser, carrying out an important ecosystemic role in the restoration of secondary tropical forests. It is considered abundant but, as fragmentation intensifies, the species is particularly vulnerable to local extinction (*Evelyn & Stiles, 2003*).

Pleistocene climatic oscillations and the complex orogeny of its distributional area shaped the phylogeography of this bat, generating two lowland lineages. The two genetic lineages, one in the Western Slope region of Mexico, and the other in the Eastern Slope region of Mexico and Central America, diverged into haplogroups around c. 0.423 Ma, and demographic expansion was detected later, after the splitting event (G Hernández-Canchola & L León-Paniagua, 2017, unpublished data). *Sturnira* is the most speciose genus of frugivorous bats. Due to its ability to colonize new areas, it adapted to produce complex groups showing different genetic lineages (*Velazco & Patterson, 2013*; *Velazco & Patterson, 2014*; G Hernández-Canchola & L León-Paniagua, 2017, unpublished data). The genus *Sturnira* involves a highly diversified and complex group of species. This speciose group of bats inhabits the entire Neotropic realm and includes three mountain basal species: *S. aratathomasi*, *S. bidens*, and *S. nana*. Also, it has been described as a clade formed by species that usually inhabit highland mountain forests: *S. bogotensis*, *S. burtonlimi*, *S. erythromos*, *S. hondurensis*, *S. koopmanhilli*, *S. ludovici*, *S. magna*, *S. mordax*, *S. oporaphilum*, *S. perla*, *S. tildae* and *S. adrianae* (*Velazco & Patterson, 2013*; *Molinari et al., 2017*). Lastly, it includes a group of species that inhabit lowland tropical forests: *S. angeli*, *S. bakeri*, *S. lilium*, *S. luisi*, *S.* new species 3, *S. paulsoni*, and *S. parvidens* (*Velazco & Patterson, 2013*).

No microsatellite molecular markers are known for *Sturnira parvidens*; our goal was to isolate and characterize polymorphic microsatellite loci for the species by using Next-Generation Sequencing. The development of these markers can be useful for understanding the genetic structure of subpopulations in its distributional range. They can be used to identify the impact of humans on the fragmentation of the populations and assess the divergent lineages formed by genetic drift. They can also be used to evaluate movements of individuals in the mosaic-fragmented landscapes, and discern the genetic component in the social structure of the population by assessing relatedness and paternity. We showed cross-species amplification in twelve species of the *Sturnira* genus, under the hypothesis of having a positive ascertainment bias due to the phylogenetic relatedness among species (*Crawford et al., 1998*; *Li & Kimmel, 2013*). Suitable cross-species amplification will facilitate studies in *Sturnira* related bat populations of Middle and South America.

MATERIALS AND METHODS

We obtained tissue samples from 26 distinct individuals of *S. parvidens* from different localities in its distributional range in Mexico. Specimens were provided by *Colección de Mamíferos del Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias-Universidad Nacional Autónoma de México*. Tissue samples were stored individually in 95% ethanol until analysis. We followed the guidelines set forth by the American Society of Mammalogists for the use of wildlife (*Gannon, Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2007*). Fieldwork was conducted with the permission of SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales de Mexico—permit FAUT-0307). Six samples were sent to the Savannah River Ecology Laboratory, for an enrichment library process. The facility follows their own protocol and provides a database of the resulting microsatellites. Meanwhile the rest of the specimens were used to standardize protocols and assess polymorphism in microsatellites.

DNA was extracted following the instructions of the Qiagen protocol (Blood and Tissue Kit, Cat No. 69504; Qiagen, Hilden, Germany) for shotgun sequences, and we used the Universal Salt Protocol to extract DNA from the remaining specimens (*Aljanabi & Martinez, 1997*). An Illumina paired-end shotgun library was prepared by shearing 1l g of tissue DNA using a Covaris S220 and following the standard protocol of the Illumina TruSeq DNA Library Kit. Five million of the resulting reads were analyzed with the program PAL_ FINDER_v0.02.03 (*Castoe et al., 2012*), in order to extract those reads that contained di-, tri-, tetra-, penta-, and hexanucleotide microsatellites.

Once positive reads were identified in PAL_FINDER, they were batched to a local installation of the program MSATCOMMANDER v 0.8.2 for primer design (*Faircloth, 2008*). We recovered 6,790 unique loci (48 hexa, 97 penta, 1,260 tetra, 1,097 tri and 4,288 dinucleotide—Fig. 1), but only 14 were chosen for PCR trials that were performed in a MultiGene^{TM} Gradient Thermal Cycler (Labnet, Edison, NJ, USA). We directly labelled forward primers (FAM) for each of the chosen loci. PCR reactions were performed in a 10 µl volume containing 30 ng of DNA, 0.2 mM of dNTPs, 10 mM of each primer, 1 Taq buffer (Buffer PCR 10×), 0.3 µL $MgCl_2$ (25 mM), and 1.0 U of FlexiTaq polymerase. PCR cycling conditions were as follows: initial denaturation at 95 °C for 3 min; followed by 30 cycles of 95 °C for 3 min, gradient temperature (ranging from 56 to 60 °C) for 30 s, and 72 °C for 2 min; extension of 68 °C for 8 min; and final ending of 4 °C. Exact annealing temperatures for each primer are given in Table 1. We visualized the PCR products by electrophoresis on 1.5% agarose gels. Markers were tested for amplification success, polymorphism and specificity in 26 individuals of *S. parvidens*.

The results of the microsatellite profiles were examined using GeneMarker® v. 2.4.2 (SoftGenetics, State College, PA, USA) and peaks were scored by hand. We obtained the number of homozygotes and heterozygotes by scoring data. We estimated the proportion of polymorphic loci and the average number of alleles per locus by using the GDA software (*Lewis & Zaykin, 2001*). We assessed the observed (H_O) and the expected heterozygosity (H_E), linkage disequilibrium, and Hardy–Weinberg proportions by using Genepop 4.2 (*Rousset, 2008*), and corroborated with Arlequin 3.5 (*Excoffier, Laval & Schneider,*

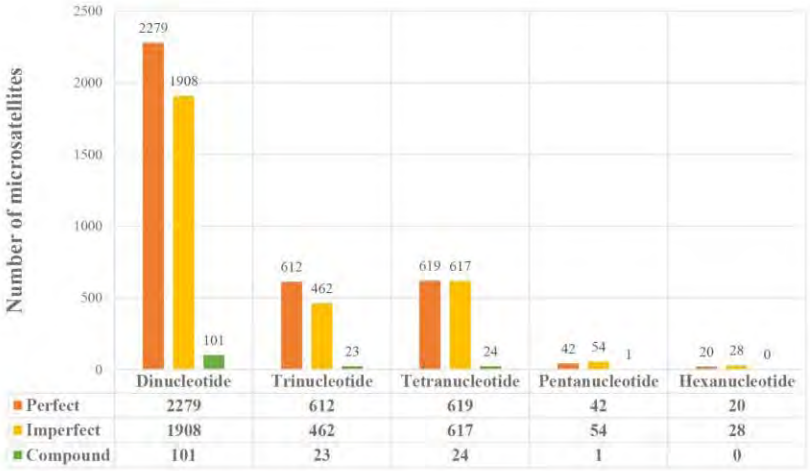

Figure 1 Potentially amplifiable loci (PAL's) with positive microsatellites found in the enriched library. Perfect, imperfect and compound loci separated out for dinucleotide to hexanucleotide microsatellite forms.

Table 1 Primer sequences and characteristics of the 14 microsatellite loci isolated for *Sturnira parvidens*. Annealing temperature not obtained (X).

Locus	Primer (Forward) (5–3′)	Primer (Reverse) (5–3′)	Motif	Annealing *T* (°C)
Spar01	6 FAM-TGCCCTGAAGAACTTTGAGC	CCCATACTTCTCCCTCACAGC	AAAG(92)	58
Spar02	6 FAM-AGAAAGAAAGGGAGGGCGG	TTCTTTATGCCCTTTGCTCTAGG	AAAG(104)	60
Spar05	6 FAM-TGCCTGCCTAGTCTGTCACC	AAGCAGTTCCCATCACATGC	ATC(33)	56
Spar06	6-FAM-CCTGGGATGAAGTTTCTGACG	GAATAATGGGAATACCAGAATAAGACG	TTC(30)	×
Spar07	6 FAM-CTCCCACGGACAATCAACG	CCCAGATTGCTGCCTCTCC	TGC(30)	56
Spar08	6 FAM-GGAGTCTCCTTCATTAAGTGCC	GGATGTGTTGTGAAGATTGTGC	ATT(30)	56
Spar09	6 FAM-AAGTCCATTTCAAGGCTGGG	CCCATCATACCCTCCTTTGC	AC(44)	60
Spar010	6 FAM-TCTGGCCTGAGGTATTTGGG	ACTGTAGCCACTTCCCTGCC	AC(44)	60
Spar011	6 FAM-AAGCCACTGCCTTGTGCC	GACTCTCTGGACATTGGCCC	TC(44)	60
Spar012	6 FAM-GGGAGTGAATGAGAAAGATAAAGTCC	CTGTCATTGCATGGGTTGG	AC(44)	60
Spar013	6 FAM-AAAGATTCCTGGAGATCATACCC	TGAATGTATCCTAGGGCGAGC	AC(42)	60
Spar014	6-FAM-TTTCTCTCACTGTCTAACTCTGCC	AGTCCTGGCAGGTGTGTCC	TC(32)	×
Spar030	6 FAM-AATGGCACCATATTATTCTACATAGG	CCGTTCTAGGCTCAGTTTCC	ATT(36)	60
Spar040	6 FAM-GACTGAGACAATTGCTTGAGATAGC	GAGTTTCAGGGAGTATTTCAGTGC	ATC(33)	60

2003). We used MICROCHECKER to screen null alleles in each locus (*Van Oosterhout et al., 2004*). We measured polymorphic information content (PIC) with Cervus 3.0.7 (*Kalinowski, Taper & Marshall, 2007*).

We probed cross-species amplification in tissues of twelve species of the genus: *S. hondurensis, S. burtonlimi, S. oporaphilum, S. mordax, S. tildae, S. erythromos,*

Table 2 Diagnostic characteristics of selected microsatellites. Number of alleles, size range, polymorphic information (PI), observed heterozygosity (H_O), expected heterozygosity (H_E), Hardy–Weinberg equilibrium (HWE), and null alleles.

Locus	GenBank accession number	No. alleles	Size range (bp)	PI	H_O	H_E	HWE	Null alleles
Spar01	KY645946	7	132–236	0.7098	0.941	0.761	0.08	×
Spar02	KY645947	6	130–222	0.6455	0.765	0.692	0.08	×
Spar05	KY645948	6	124–226	0.6069	0.412	0.699	0.05	✓
Spar07	KY645949	10	121–226	0.8028	0.824	0.865	0.18	✓
Spar08	KY645950	11	130–382	0.8052	0.800	0.860	0.13	×
Spar09	KY645951	13	134–230	0.8864	0.875	0.933	0.11	×
Spar010	KY645952	12	132–236	0.8698	0.882	0.919	0.08	×
Spar011	KY645953	8	124–222	0.8125	0.588	0.863	0.12	×
Spar012	KY645954	8	128–214	0.7068	0.750	0.772	0.08	×
Spar013	KY645955	10	124–220	0.8577	0.500	0.867	0.05	✓
Spar030	KY645957	6	133–169	0.7088	0.741	0.735	0.08	×
Spar040	KY645958	6	124–190	0.6721	0.662	0.669	0.08	×

S. bogotensis, *S. magna*, *S. new species 3*, *S. luisi*, *S. lilium*, and *S. bakeri* (Supplemental Information 1). All polymorphic loci were tested in the mentioned species by using similar PCR conditions. We followed the ascertainment bias hypothesis of broad amplification in similar phylogenetic species (*Schlötterer, 2000*).

RESULTS

We obtained a total of 6,790 potentially amplifiable loci (PALs), containing perfect, imperfect, and compound microsatellites (Fig. 1). Dinucleotide microsatellites were the most abundant (4,288), followed by tetra (1,260); hexa microsatellites were the least abundant in our readings (48). PCR reactions showed that of the 14 loci tested, two were non-specific or monomorphic, and only 12 loci were polymorphic such that we were able to get proper amplification (Table 1). Annealing temperature ranged from 56 to 60 °C.

We found moderate levels of allelic richness, with an average of 8.8 alleles per locus in the representative selection from the wide area of the distribution of *Sturnira parvidens*. Polymorphic information content (PIC) presented values above 0.5 showing a significant content of alleles per locus. Allele frequencies showed a remarkable diversity of alleles per locus, driving a superior number of valuable loci to be used in different genetic analyses (Supplemental Information 2). No evidence of linkage disequilibrium was found on the analyzed loci. We did not observe any loci out of Hardy–Weinberg equilibrium. Levels of expected heterozygosity (H_E) ranged from medium to high for all markers (mean $H_E = 0.79$, and mean $H_O = 0.72$). In the majority, there was no evidence of null alleles, but three loci (Spar05, Spar07, Spar013) showed significant frequencies of null alleles (above 15%–Table 2).

Cross-species amplification showed differences for the twelve related species (Table 3). *S.* new species 3 presented the largest number of amplified microsatellites (8), followed by *S. bakeri* (7). *S. mordax* had the lowest number of amplified loci (4).

Table 3 Cross-species amplifications of the designed primers for *S. parvidens*. We followed same PCR conditions in the twelve related species. (×) no positive amplification, (✓p) positive polymorphic amplification, (✓m) positive monomorphic amplification, (✓*) polymorphism not proven because PCR conditions were not standardized.

Locus	*S. hondurensis* ($n=3$)	*S. burtonlimi* ($n=3$)	*S. oporaphilum* ($n=1$)	*S. mordax* ($n=2$)
Spar01	×	✓p	×	×
Spar02	✓p	×	✓*	×
Spar05	✓p	✓p	✓*	✓*
Spar07	×	×	×	×
Spar08	✓*	✓p	✓*	✓p
Spar09	×	✓p	✓*	✓*
Spar010	×	✓*	✓*	×
Spar011	✓*	✓p	✓*	✓p
Spar012	✓m	×	✓*	×
Spar013	×	×	✓*	×

S. tildae ($n=1$)	*S. erythromos* ($n=1$)	*S. magna* ($n=1$)	*S. bogotensis* ($n=1$)	*S.* newspecies_3 ($n=3$)	*S. luisi* ($n=3$)	*S. lilium* ($n=3$)	*S. bakeri* ($n=2$)
×	×	×	×	✓p	×	✓*	✓*
×	×	✓*	×	✓*	×	×	✓*
✓*	×	✓*	×	✓*	✓*	✓*	×
×	×	×	×	✓p	×	×	✓p
✓*	✓*	×	✓*	✓p	✓*	✓*	✓p
✓*	✓*	×	✓*	✓p	✓*	✓*	✓p
✓*	✓*	✓*	✓*	✓p	✓*	✓p	✓p
✓*	✓*	✓*	✓*	✓*	✓p	✓*	✓*
✓*	✓*	✓*	✓*	×	×	×	×
✓*	✓*	✓*	✓*	×	×	×	×

DISCUSSION

Next Generation Sequencing allowed the project to obtain a large number of microsatellite loci for *Sturnira parvidens*. This method has been probed for several bat species, and it is becoming a standard method for acquiring specific molecular markers (*McCulloch & Stevens, 2011*). Given the natural applicability of microsatellites to solve ecological questions, these molecular markers have emerged as a multipurpose indicator for ecological applications (*Zane, Bargelloni & Patarnello, 2002*; *Selkoe & Toonen, 2006*). Its applicability spreads to different academic fields such as population genetics, behavioral ecology, genomics, phylogenies, etc.

Our microsatellites conformed to the normal standard measures (*Balloux & Lugon-Moulin, 2002*). These indicators provide a straightforward approach for describing genetic variation due to the high level of existing alleles. Low allelic richness can affect accuracy in estimating population genetic parameters, leading to significant errors in assessing genetic diversity of target populations (*Bashalkhanov, Pandey & Rajora, 2009*). Here, we present a novel set of microsatellite loci with the potential to estimate genetic diversity in a non-model species. Standard measures for our microsatellites may have important

implications in the evolutionary biology of the target species, because they can be used to develop conservation strategies for Neotropical bats. Highly informative microsatellites have been used to assess genetic diversity in a broad range of bat populations and to propose measures for conservation (i.e., *Rossiter et al., 2000*; *Romero-Nava, León-Paniagua & Ortega, 2014*; *Korstian, Hale & Williams, 2015*).

Amplified microsatellites for *S. parvidens* presented levels of polymorphism and heterozygosity similar to those found in other bat species (i.e., *Artibeus jamaicensis*—*Ortega et al., 2002*; *Rhinolophus ferrumequinum*—*Dawson et al., 2004*; *Desmodus rotundus*-*Piaggio, Johnston & Perkins, 2008*; *Corynorhinus* spp.—*Lee, Howell & Van Den Bussche, 2011*; *Myotis* spp.—*Jan et al., 2012*; *Carollia castanea*—*Cleary, Waits & Hohenlohe, 2016*).

Microsatellite markers are widely used to infer levels of genetic diversity in natural populations. Molecular markers are not always developed for the target species and the use of microsatellite loci from related species can be accurate. Ascertainment bias limited the microsatellite-based amplification due to the particular selection of polymorphic markers in the target species, plus the reduced sensitivity of the markers due to the phylogenetic constrictions of the particular evolutionary traits of each sister species (*Crawford et al., 1998*; *Schlötterer, 2000*; *Li & Kimmel, 2013*). The bias leads to a lower average allele length due to the phylogenetic restriction provided by the unique evolutionary history of each species (*Li & Kimmel, 2013*). We tested the potential use of our markers in related species, finding multilocus heterozygosities inside the *Sturnira* genus. This positive effect suggests the use of the developed markers to extrapolate genetic diversity in future studies for this highly speciose genus, in which the past demographic shared histories barely affect the cross-species amplification consolidation.

CONCLUSIONS

We used Illumina Paired-Sequences to efficiently develop microsatellite loci for *Sturnira parvidens*. We formed a genomic library to obtain 12 specific and polymorphic microsatellites for this bat. Microsatellites showed high allelic richness per locus, showing their effectiveness for further studies (i.e., population genetics, behavioral ecology, etc.). Cross-species amplification was effective for the 12 related species, but with no positive amplifications in several cases.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Edgar G. Gutiérrez and Giovani Hernández Canchola conceived and designed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Livia S. León Paniagua and Jorge Ortega conceived and designed the experiments, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Norberto Martínez Méndez conceived and designed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

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DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

Gen Bank: Spar01 KY645946, Spar02 KY645947, Spar05 KY645948, Spar07 KY645949, Spar08 KY645950, Spar09 KY645951, Spar010 KY645952, Spar011 KY645953, Spar012 KY645954, Spar013 KY645955, Spar030 KY645957, Spar040 KY645958.

Data Availability

The following information was supplied regarding data availability:

The raw data has been supplied as a Supplementary File.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.3367#supplemental-information.

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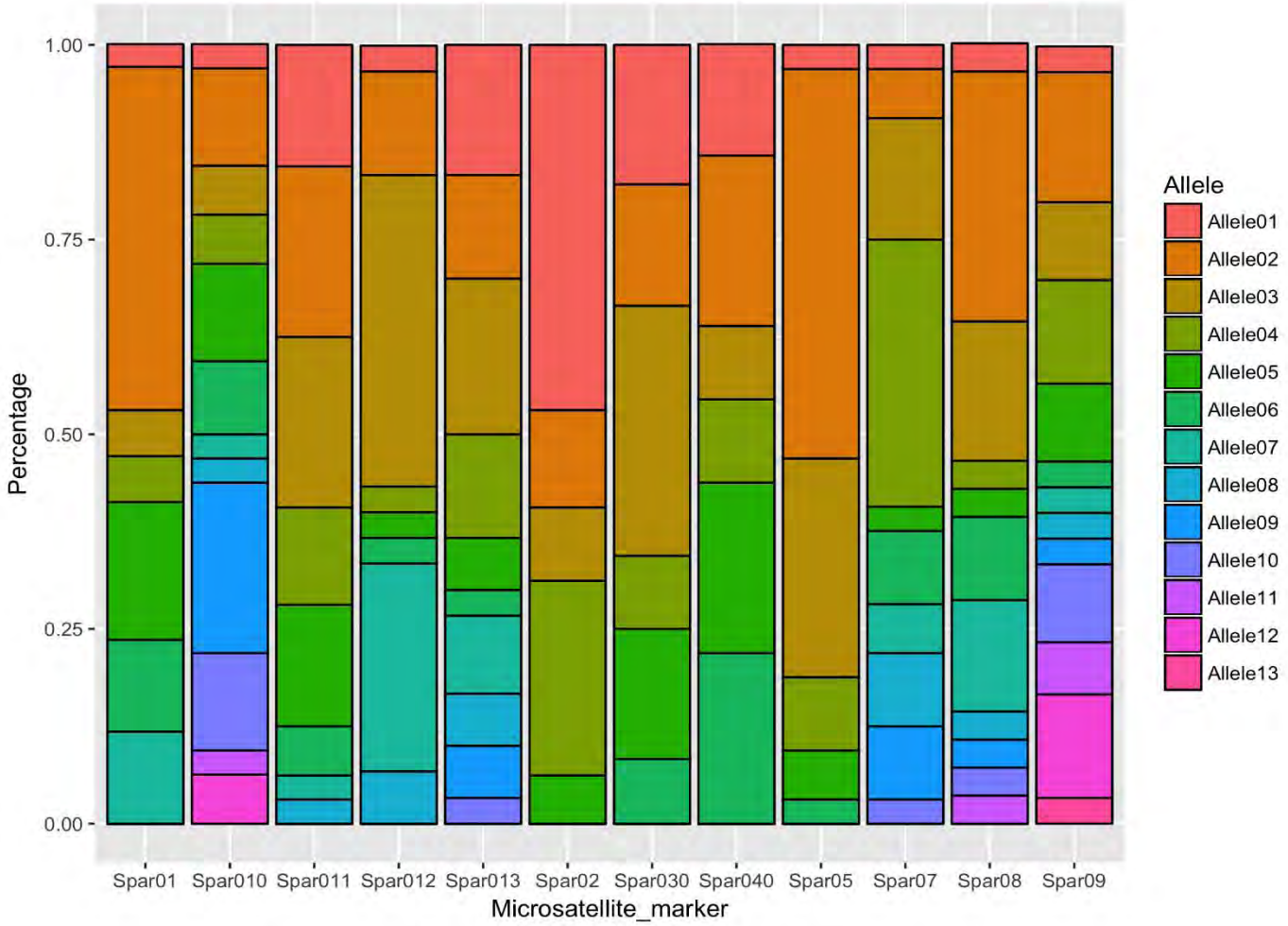
Supplementary material 1: Tissues supplemented by different Museums to probe cross-species amplification and library enrichment. We are presenting museum; voucher, tissue or collector number; species and specific use of the tissue. Acronyms of museums are. MZFC (Museo de Zoología de la Facultad de Ciencias), MZUCR (Museo de Zoología de la Universidad de Costa Rica), FMNH (Field Museum of Natural History), TTU (Texas Tech University), and LSUMZ (Lousiana State University Museum of Zoology).

Museum	Sample	Species	Utility
MZFC-M	GHC396	*S. hondurensis*	Cross amplification
MZFC-M	TACM073	*S. hondurensis*	Cross amplification
MZFC-M	MRM166	*S. hondurensis*	Cross amplification
MZUCR	TUCR18	*S. burtonlimi*	Cross amplification
MZUCR	TUCR20	*S. burtonlimi*	Cross amplification
MZUCR	TUCR48	*S. burtonlimi*	Cross amplification
FMNH	174845	*S. oporaphilum*	Cross amplification
MZUCR	TUCR27	*S. mordax*	Cross amplification
MZUCR	TUCR29	*S. mordax*	Cross amplification
FMNH	174871	*S. tildae*	Cross amplification
FMNH	174803	*S erythromos*	Cross amplification
FMNH	128785	*S. bogotensis*	Cross amplification
FMNH	174833	*S. magna*	Cross amplification
TTU	TK104211	*S.* new species 3	Cross amplification
TTU	TK104337	*S.* new species 3	Cross amplification
TTU	TK104349	*S.* new *species* 3	Cross amplification
LSUMZ	LSUMZ393	*S. luisi*	Cross amplification
LSUMZ	LSUMZ394	*S. luisi*	Cross amplification
LSUMZ	LSUMZ529	*S. luisi*	Cross amplification
TTU	TK56609	*S. lilium*	Cross amplification
TTU	TK56808	*S. lilium*	Cross amplification
TTU	TK56950	*S. lilium*	Cross amplification
TTU	TK104623	*S. bakeri*	Cross amplification
TTU	TK104662	*S. bakeri*	Cross amplification
TTU	TK136986	*S. parvidens*	Amplification
MZFC-M	GHC009	*S. parvidens*	Illumina paired-end sequencing and amplification
MZFC-M	GHC032	*S. parvidens*	Amplification
MZFC-M	GHC060	*S. parvidens*	Illumina paired-end sequencing and amplification

MZFC-M	GHC072	*S. parvidens*	Illumina paired-end sequencing and amplification
MZFC-M	GHC103	*S. parvidens*	Amplification
MZFC-M	GHC213	*S. parvidens*	Amplification
MZFC-M	GHC214	*S. parvidens*	Amplification
MZFC-M	GHC240	*S. parvidens*	Illumina paired-end sequencing and amplification
MZFC-M	GHC445	*S. parvidens*	Amplification
MZFC-M	MAG011	*S. parvidens*	Amplification
MZFC-M	MAG014	*S. parvidens*	Amplification
MZFC-M	MCyT053	*S. parvidens*	Amplification
MZFC-M	MCHAM079	*S. parvidens*	Amplification
MZFC-M	MRM075	*S. parvidens*	Illumina paired-end sequencing and amplification
MZFC-M	DOR013	*S. parvidens*	Illumina paired-end sequencing and amplification
MZFC-M	151CAS	*S. parvidens*	Amplification
MZFC-M	210HRP	*S. parvidens*	Amplification
MZFC-M	MBB012	*S. parvidens*	Amplification
MZFC-M	MCP079	*S. parvidens*	Amplification

Supplementary material 2: Allelic frequencies of amplified microsatellite loci**,** colors represent the absolute frequencies of the different alleles.



Raw data

Spar01

TGCCCTGAAGAACTTTGAGCAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGA
AAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GCCCATACTTCTC

CCTCACAGC

Spar02

AGAAAGAAAGGGAGGGCGGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAG
AAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
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GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAA
GAAAGAAAGAAAG

AAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGAAAGTTCTTTATGCCCTTTGCTCTAGG

Spar05

TGCCTGCCTAGTCTGTCACCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATC
ATC

ATCATCATCATCATCATCATCATCATCATCATCATCATCATCAAGCAGTTCCCATCACATGC

Spar06

CCTGGGATGAAGTTTCTGACGTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTC
C

TTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCGAATAATGGGAATACCAGAATAAGACG

Spar07

CTCCCACGGACAATCAACGTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTGCTG
CTGCTGC

TGCTGCTGCTGCTGCTGCTGCTGCTGCTGCCCCAGATTGCTGCCTCTCC

Spar08

GGAGTCTCCTTCATTAAGTGCCATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTATT
ATT

ATTATTATTATTATTATTATTATTATTATTGGATGTGTTGTGAAGATTGTGC

Spar09

AAGTCCATTTCAAGGCTGGGACACACACACACACACACACACACACACACACACACACACACACACACACAC
ACACACAC

ACACACACACACACACACACACACACACCCCATCATACCCTCCTTTGC

Spar010

TCTGGCCTGAGGTATTTGGGACACACACACACACACACACACACACACACACACACACACACACACACAC
ACACACAC

ACACACACACACACACACACACACACACACTGTAGCCACTTCCCTGCC

Spar011

AAGCCACTGCCTTGTGCCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTC
CTC

TCTCTCTCTCTCTCTCTCTCTCTCTCGACTCTCTGGACATTGGCCC

Spar012

GGGAGTGAATGAGAAAGATAAAGTCCACACACACACACACACACACACACACACACACACACACACACACACACAC

ACACACACACACACACACACACACACACACACACACCTGTCATTGCATGGGTTGG

Spar013

AAAGATTCCTGGAGATCATACCCACACACACACACACACACACACACACACACACACACACACACACACACACAC

ACACACACACACACACACACACACACACTGAATGTATCCTAGGGCGAGC

Spar014

TTTCTCTCACTGTCTAACTCTGCCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCTCT
CTCT

CTCTCTCTCTCTCTCTCTCTCTCTCTCAGTCCTGGCAGGTGTGTCC

Spar030

AATGGCACCATATTATTCTACATAGGATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTA
TTATT

ATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTATTCCGTTCTAGGCTCAGTTTCC

Spar040

GACTGAGACAATTGCTTGAGATAGCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATC
ATCATC

ATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCATCGAGTTTCAGGGAGTATTTCAGTGC