

REGULAR PAPER

Genetic differentiation among populations of the blackfin goodea *Goodea atripinnis* (Cyprinodontiformes: Goodeidae): implications for its evolutionary history

Rosa Gabriela Beltrán-López^{1,2}  | Omar Domínguez-Domínguez^{3,4}  |
 Kyle R. Piller⁵  | Humberto Mejía-Mojica² | Adán Fernando Mar-Silva^{3,6} |
 Ignacio Doadrio⁷ 

¹Programa Institucional de Doctorado en Ciencias Biológicas, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Mexico

²Laboratorio de Ictiología, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Mexico

³Laboratorio de Biología Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Mexico

⁴Laboratorio Nacional de Análisis y Síntesis Ecológica para la Conservación de Recursos Genéticos de México, Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Mexico

⁵Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana

⁶Programa Institucional de Maestría en Ciencias Biológicas, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Mexico

⁷Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

Correspondence

Omar Domínguez-Domínguez, Laboratorio de Biología Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, 58030, México. Email: omar.dominguez@umich.mx

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Abstract

Central Mexico is characterized by a complex topography that is the result of historic and contemporary tectonic and climatic factors. These events have influenced the evolutionary history of numerous freshwater fishes in the region. Nonetheless, recent studies have shown that life-history traits and ecological characteristics of species may influence dispersal capabilities and the degree of genetic connectivity. *Goodea* (Cyprinodontiformes: Goodeidae) is one of the most widely distributed and environmentally tolerant genera of goodeids. In this study, the authors analysed variation in the mitochondrial cytochrome b gene to evaluate the phylogeographic relationships, genetic structure, genetic diversity and demographic history of *Goodea* from across its distribution range. They found low genetic differentiation and identified shared haplotypes among several regions. Geographic segregation was found in samples southwest and northeast of the Lower Lerma region, with some internal isolated groups showing phylogeographic differentiation and unique haplotypes. The AMOVA best explained genetic structure when grouped by haplogroups rather than when grouped by recognized biogeographic regions. Several regions showed null genetic diversity, raising the possibility of dispersal mediated by humans. Finally, Bayesian Skyline Plot analysis showed a population expansion for the Southwest haplogroup, except for the Armería population and sub-group II of the Northeast haplogroup. All this suggests a recent colonization of *Goodea atripinnis* throughout some of the biogeographic regions currently inhabited by this species.

KEYWORDS

endemic fish, haplogroups, life-history traits, phylogeography, widespread species

1 | INTRODUCTION

The distribution of genetic variation in freshwater organisms is mainly affected by the geologic evolution of the basins where they occur,

frequently resulting in strong genetic structure among populations as a result of their confinement to particular hydrological systems (Faulks *et al.*, 2010; Loxterman & Keeley, 2012). For widely distributed freshwater fishes, genetic differentiation patterns are more frequently

linked with historical geomorphological processes of the drainages than present-day configurations (Beltrán-López *et al.*, 2018; Birmingham & Martin, 1998; Domínguez-Domínguez *et al.*, 2008a; Hewitt, 2000, 2004; Perea *et al.*, 2016; Pérez-Rodríguez *et al.*, 2009).

For its high geological dynamism, Mexico is considered a model region for studying how ecological and biological traits affect the genetic structure or connectivity of species (Mastretta-Yanes *et al.*, 2015). Under this context, central Mexico is characterized by a complex topography as a result of its rich tectonic and climatic history, with the Trans Mexican Volcanic Belt (TMVB) being one of the most important geological features of this region (Domínguez-Domínguez & Pérez-Ponce de León, 2009). Since the Neogene, the uplift of the TMVB has promoted a long history of genesis and modification of water drainages and the formation of new geographic barriers and montane habitats. These geologic events have had a significant impact on the diversification of aquatic taxa in the region (Anducho-Reyes *et al.*, 2008; Beltrán-López *et al.*, 2018; Domínguez-Domínguez *et al.*, 2008a, 2010, 2016; Ferrusquía-Villafranca, 1993; Huidobro *et al.*, 2006; Lyons *et al.*, 2019; Mateos *et al.*, 2002, 2019; Pérez-Rodríguez *et al.*, 2009, 2016).

On the contrary, recent studies have demonstrated that life-history traits and ecological characteristics of species may also influence dispersal capabilities, which, in turn, can affect the genetic connectivity of their populations (Betancourt-Resendes *et al.*, 2018; Goto & Andoh, 1990). In this sense, dispersal and colonization capabilities can play important roles in the occupancy of new habitats and in the geographic distribution of freshwater fishes (Clobert *et al.*, 2001).

The goodeines (subfamily Goodeinae) are one of the most prevalent groups of freshwater fishes in central Mexico. Several species within the subfamily are widespread, whereas others are restricted to a few river systems or even a single spring (Domínguez-Domínguez *et al.*, 2010; Foster & Piller, 2018; Lyons *et al.*, 2019; Miller *et al.*, 2005; Parker *et al.*, 2019). The goodeines with their widespread distribution across central Mexico, high species diversity, wide range of body shapes (as influenced by habitat) and exceptional ecomorphological disparity are considered a model system for understanding adaptive radiation and the biogeographic history of one of the most important faunal transitional zones in the world (Doadrio & Domínguez, 2004; Domínguez-Domínguez *et al.*, 2006, 2010; Foster & Piller, 2018; Helmstetter *et al.*, 2016; Parker *et al.*, 2019).

Evolutionary studies of several goodeines species have found high genetic structure and divergence among genera, species and populations, as was the case of *Zoogoneticus quitzeonensis* (Bean 1898), *Xenotoca eiseni* (Rutter 1896) and *Ilyodon* species (Beltrán-López *et al.*, 2017; Domínguez-Domínguez *et al.* 2008a, 2008b, 2016; Piller *et al.*, 2015).

Although not common, examples of null or low genetic differentiation, shared haplotypes among isolated drainages and recent isolation events between freshwater fish species in the region have been identified (Beltrán-López *et al.*, 2018; Betancourt-Resendes *et al.*, 2018). For goodeines, some patterns can be explained by human-mediated dispersion, recent connections or high dispersion capability of the species (Corona-Santiago *et al.*, 2015; Ornelas-García *et al.*, 2012).

Among the Goodeinae, the genus *Goodea* has the widest geographic distribution (Miller *et al.*, 2005), as well as high tolerance to a

wide range of ecological conditions (De la Vega-Salazar, 2006). Morphological differences among populations have been recognized (Miranda *et al.*, 2010), and at least three species have been described: *Goodea atripinnis* Jordan 1880, from the Lerma River basin, which drains to the Pacific slope; *Goodea luitpoldii* (Steindachner 1894), from the endorheic Lake Pátzcuaro and *Goodea gracilis* (Hubbs and Turner 1939), from the Pánuco River basin on the Atlantic slope. Despite the recognition of these three described species, recent molecular studies using a reduced number of samples and a single mitochondrial gene have concluded that *Goodea* is comprised of only a single species, *G. atripinnis* (Domínguez-Domínguez *et al.*, 2010; Foster & Piller, 2018; Webb *et al.*, 2004). Other authors, however, have proposed to include the Pánuco River basin population as an independent Evolutionarily Significant Unit rather than a separate species (Lyons *et al.*, 2019).

The objective of this study is to examine the phylogeographic relationships, genetic structure, genetic diversity and demographic history of populations of *G. atripinnis* from across its entire range, as well as to compare these evolutionary patterns with those found in previous studies of goodeines (Domínguez-Domínguez *et al.*, 2008a) and other co-distributed fish species, such as poeciliids (Beltrán-López *et al.*, 2018) and cyprinids (Pérez-Rodríguez *et al.*, 2009; Schönhuth & Doadrio, 2003). To accomplish this, the authors of this study sampled extensively throughout the distribution range of *Goodea* and included many individuals per population to alleviate the small sample size issues of previous studies (Doadrio & Domínguez, 2004; Domínguez-Domínguez *et al.*, 2010; Webb *et al.*, 2004).

2 | MATERIALS AND METHODS

2.1 | Ethical statement

The care and use of animals complied with SEMARNAT animal welfare laws, guidelines and policies as approved by SEMARNAT-SGA/DGVS/2009/19, SEMACDET-OS-0084/2019.

2.2 | Fish sampling and DNA isolation

Three hundred eighteen specimens were obtained from 72 localities in 23 biogeographical regions proposed for central Mexico by Domínguez-Domínguez *et al.* (2006). The samples include rivers and lakes and cover the entire distributional range of *G. atripinnis* (Figure 1; Table 1). Fish were captured under the following permissions: SEMARNAT-SGA/DGVS/2009/19, SEMACDET-OS-0084/2019 by electrofishing and through the use of seine nets. Captured fish were anaesthetized with tricaine-mesylate (MS-222) before tissueing and subsequent preservation. Additional specimens were obtained directly from local fishermen. Pectoral fin clips were taken and preserved in absolute ethanol, frozen at -75°C and deposited in the tissue bank of the Aquatic Biology laboratory of the Universidad Michoacana de San Nicolás de Hidalgo (Mexico) and in DNA and tissue collection of the Museo Nacional de Ciencias Naturales (Spain).

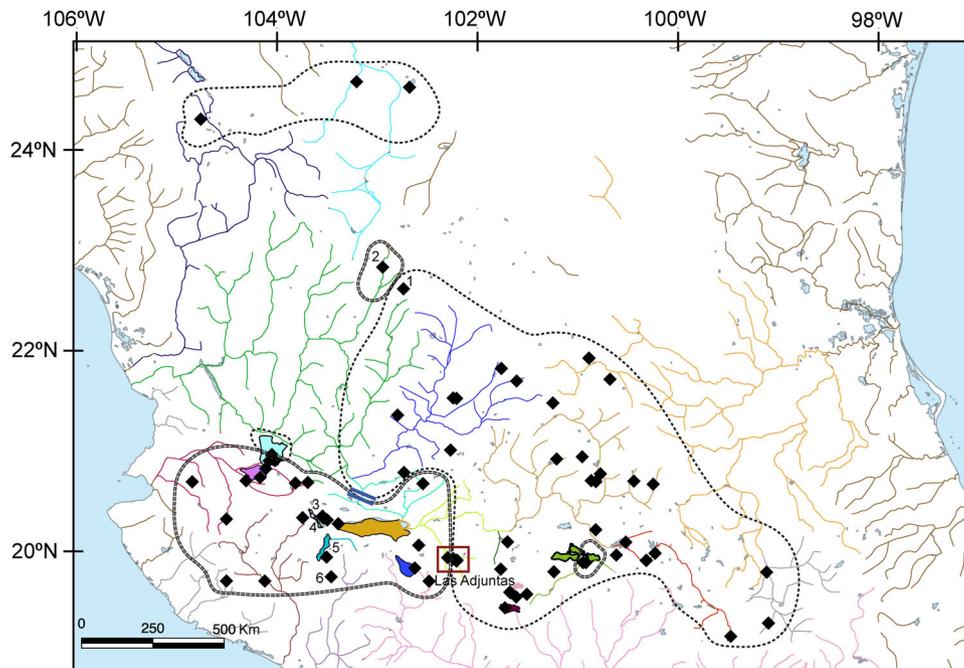


FIGURE 1 Geographic location of *Goodea atripinnis* samples used in this study. Lines represent the geographic distribution of the two recovered haplogroups obtained in the haplotypes network. The abbreviations of the biogeographical regions are: MEZ: Mezquital river, AGU: Aguanaval river, 1 JUC: Juchipila River, 2 BOL: Bolaños River, AME: Ameca River, LLE: Lower Lerma River, PAT: Lake Pátzcuaro, ZAC: Lake Zacapu, CHA: Lake Chapala, MAG: Lake Magdalena, ARM: Armería River, BAL: Balsas River, COT: Lake Cotija, CUI: Lake Cuitzeo, SAN: Santiago River, VER: Verde River, ETZ: Etzatlán-San Marcos, MLE: Middle Lerma River, 3 ATO: Lake Atotonilco, 4 SMA: Lake San Marcos, 5 SAY: Lake Sayula, 6 ZAP: Lake Zapotlán (these last four lakes corresponded with the Sayula region), ZIR: Lake Zirahuén, ULE: Upper Lerma River, VME: Valley of Mexico and, PAN: Pánuco River (■) MEZ (■) AGU (■) 1 JUC (■) 2 BOL (■) AME (■) LLE (■) PAT (■) ZAC (■) CHA (■) MAG (■) ARM (■) BAL (■) COT (■) CUI (■) SAN (■) VER (■) ETZ (■) MLE (■) 3 ATO (■) 4 SMA (■) 5 SAY (■) 6 ZAP (■) ZIR (■) ULE (■) VME (■) PAN (■) (---) Southwest haplogroup (---) Northeast haplogroup (■) Las Adjuntas (---) Salto de Juanacatlán

Some specimens were also deposited in the fish collection of the Universidad Michoacana de San Nicolás de Hidalgo. Tissues for DNA extraction were digested with ATL QIAGEN Buffer and Proteinase K and purified with BioSprint DNA Blood Kit QIAGEN according to the manufacturer's instructions.

2.3 | Locus amplification and sequencing

PCR was performed to amplify the cytochrome b gene (*cytb*) with the primers GLuDG (Palumbi *et al.*, 1991) and H16460 (Perdices *et al.*, 2002). The PCR reaction consisted of a 12.5 µl final volume reaction containing 4.25 µl of nuclease-free water, 0.5 µl of each 0.2 µM primer, 6.25 µl of Dream Taq Green PCR Master Mix 2x containing DreamTaq DNA polymerase, 2x Dream Taq Green buffer, dATP, dCTP, dGTP and dTTP, 0.4 mM each, and 4 mM of MgCl₂ (Thermo Scientific, Waltham, MA, USA) and 1 µl (c. 10–100 ng) of DNA template. The PCR procedure was performed for 2 min at 94°C followed by 35 cycles of 45 s at 94°C for DNA denaturation, 1 min at 46.5°C for primer alignment, 1.5 min at 72°C for synthesis and a final extension of 5 min at 72°C. After checking the PCR products by electrophoresis in agarose gel of 1.5%, amplicons were purified using ExoSAP-IT (USB Corp.

Cleveland, OH, USA) and submitted to Macrogen Inc. (the Netherlands) for sequencing. Manual alignment of sequences was implemented in Mega v7.0 (Kumar *et al.*, 2016). Only sequences corresponding to different haplotypes were deposited in GenBank under the accession numbers MT953509–MT953566 (see Supporting Information Table TABLE S1).

2.4 | Haplotype network, population structure and genetic distances

To evaluate the geographic correspondence of haplotypes for all populations of *G. atripinnis*, the network estimation was reconstructed using the median-joining algorithm as implemented in PopArt v1.7 (<http://popart.otago.ac.nz>).

To analyse the genetic structure of populations of *G. atripinnis*, the authors conducted analyses of molecular variance (AMOVA) using Arlequin v3.5.1.3 (Excoffier & Lischer, 2010) at four hierarchical levels: (a) the discrete biogeographical regions proposed by Domínguez-Domínguez *et al.* (2006), (b) Southwest and Northeast haplogroups + Armería River; (c) Northeast sub-group I + Northeast sub-group II + Southwest + Armería River; and (d) without *a priori* grouping (all specimens constituting one gene pool). Components of the fixation

TABLE 1 Information on sample localities and sequences

Locality	Basin	Biogeographic region	Number of sequences	Geographical coordinates
Presa la Quemada	Lake Magdalena	Magdalena	5	20° 57' 51.05" N, 104° 3' 8.34" W
Los Venados	Lake Magdalena	Magdalena	7	20° 54' 14.2" N, 104° 1' 11.6" W
Lago de Magdalena	Lake Magdalena	Magdalena	9	20° 54' 3.69" N, 104° 4' 45.62" W
El Moloya	Lake Magdalena	Magdalena	11	20° 57' 51.05" N, 104° 3' 8.34" W
Presa La Luz	Duero River	Lower Lerma	2	19° 56' 12.4" N, 102° 17' 55.3" W
Las Adjuntas	Duero River	Lower Lerma	8	19° 54' 39.9" N, 102° 12' 20" W
El Platanal	Duero River	Lower Lerma	6	19° 55' 40.7" N, 102° 14' 30.3" W
Pateo	Lower Lerma	Lower Lerma	1	19° 54' 33.1" N, 100° 19' 5.1" W
Camécuaro	Lake Camécuaro	Lower Lerma	3	19° 54' 9.8" N, 102° 12' 35.27" W
Amatlán de Cañas	Ameca	Ameca	2	20° 42' 13.7" N, 104° 18' 34.4" W
El Rincón	Ameca	Ameca	1	20° 41' 34.8" N, 104° 50' 47.1" W
Tala, Río Salado	Ameca	Ameca	5	20° 41' 12.1" N, 103° 41' 36.3" W
Teuchitlán	Cocula-La Vega	Ameca	5	20° 40' 46.8" N, 103° 50' 59.2" W
Xochimilco	Canal de Xochimilco	Valle de México	2	19° 17' 3" N, 99° 6' 7.62" W
Presa del Carmen	Pánuco	Pánuco	6	20° 40' 8.1" N, 100° 15' 6.73" W
Zumpango	Pánuco	Pánuco	4	19° 47' 31.6" N, 99° 7' 1" W
San Ildefonso	Pánuco	Pánuco	1	19° 57' 43.2" N, 100° 37' 1.27" W
Tierra Quemada	Pánuco	Pánuco	1	21° 42' 53.9" N, 100° 41' 15.9" W
Jesús María	Pánuco	Pánuco	5	21° 55' 24.3" N, 100° 54' 39.9" W
Jesús María-Villa de Reyes	Pánuco	Pánuco	5	21° 55' 32.3" N, 100° 54' 39.5" W
Santa Clara	Aguanaval	Aguanaval	12	24° 40' 47.5" N, 103° 13' 36.2" W
Presa el Tecolote	Verde	Verde	1	21° 31' 25.1" N, 102° 13' 25.2" W
Arroyo el Tecolote	Verde	Verde	3	21° 31' 38.4" N, 102° 15' 22.1" W
Presa La Paz	Verde	Verde	2	21° 49' 21.0" N, 101° 46' 13.7" W
Guadalupe Victoria	Verde	Verde	1	21° 41' 49.3" N, 101° 37' 21.3" W
San Julián-San Miguel	Verde	Verde	2	21° 0' 32.7" N, 102° 17' 47.3" W
Bordo en Chimaliquin	Verde	Verde	1	21° 21' 24" N, 102° 48' 6.8" W
Presa El Tesorero	Bolaños	Bolaños	3	22° 49' 53.6" N, 102° 57' 12.7" W
Urideo, ojo de agua el Capulin	Middle Lerma	Middle Lerma	2	20° 12' 52.2" N, 100° 50' 43.4" W
Arroyo Neutla	Neutla	Middle Lerma	2	20° 41' 41.5" N, 100° 50' 48.8" W
Carretera San Miguel-Comonfort	Middle Lerma	Middle Lerma	2	20° 46' 17.8" N, 100° 47' 30.0" W
Afluente Neutla	Neutla	Middle Lerma	1	20° 42' 16.5" N, 100° 52' 1.6" W
Río San José del Rodeo	Middle Lerma	Middle Lerma	7	20° 55' 12.2" N, 101° 13' 19.9" W
Río Xoconostle-San Juan	Laja	Middle Lerma	1	20° 56' 31.5" N, 100° 58' 38" W
Manantial Andrés-Figueroa	San Marcos	Sayula	5	20° 20' 0.4" N, 103° 34' 97.6" W
Depósito Santa Catarina	San Marcos	Sayula	1	20° 21' 3.6" N, 103° 33' 11.6" W
Canal Presa Buena Vista	Atotonilco	Sayula	7	20° 20' 5.8" N, 103° 45' 19.7" W
Lago Atotonilco	Atotonilco	Sayula	4	20° 18' 45.6" N, 103° 31' 59.3" W
Presa Buena Vista	Atotonilco	Sayula	4	20° 20' 5.2" N, 103° 45' 20.2" W
Lago de Zapotlán	Zapotlán	Sayula	9	19° 44' 44.9" N, 103° 28' 22.4" W
Lago de Sayula	Sayula	Sayula	10	19° 56' 32" N, 103° 31' 36.7" W
Lago de Chapala	Chapala	Chapala	2	20° 16' 30.4" N, 103° 24' 37.1" W
Los Negritos	Chapala	Chapala	2	20° 3' 36.3" N, 102° 36' 46.1" W
Chiquimitio	Cuitzeo	Cuitzeo	4	19° 47' 44.6" N, 101° 15' 41.1" W
Río Queréndaro	Cuitzeo	Cuitzeo	7	19° 53' 13.9" N, 100° 56' 52.2" W
Desembocadura Río Queréndaro	Cuitzeo	Cuitzeo	2	19° 53' 14.5" N, 100° 57' 7.1" W

TABLE 1 (Continued)

Locality	Basin	Biogeographic region	Number of sequences	Geographical coordinates
Manantial Chapultepec	Pátzcuaro	Pátzcuaro	8	19° 34' 19.1" N, 101° 31' 29.3" W
Embarcadero Principal	Pátzcuaro	Pátzcuaro	3	19° 32' 42.9" N, 101° 37' 4.2" W
Erongacúaro	Pátzcuaro	Pátzcuaro	2	19° 35' 12.6" N, 101° 41' 50.21" W
Napizaro	Pátzcuaro	Pátzcuaro	3	19° 35' 30" N, 101° 41' 16.5" W
Presa Melchor Ocampo	Angulo-Lerma	Zacapu	12	20° 5' 36.5" N, 101° 43' 57.4" W
La Zarcita	Angulo-Lerma	Zacapu	2	19° 49' 19" N, 101° 47' 51" W
Tocumbo	Balsas	Balsas	7	19° 42' 7" N, 102° 30' 60" W
Presa San Juanico	Cotija	Cotija	3	19° 49' 57.4" N, 102° 38' 25.8" W
San Sebastián	Etzatlán-San Marcos	Etzatlán-San Marcos	9	20° 49' 25" N, 104° 7' 10.8" W
Presa San Rafael	Etzatlán-San Marcos	Etzatlán-San Marcos	4	20° 44' 8.3" N, 104° 11' 49.7" W
Puente Malpaso	Juchipila	Juchipila	11	22° 36' 57.2" N, 102° 45' 39.5" W
Tepatitlán	Santiago-Chapala	Grande de Santiago	4	20° 47' 6.8" N, 102° 45' 58.7" W
San Antonio, Tepatitlán	Santiago-Chapala	Grande de Santiago	7	20° 40' 27.2" N, 102° 33' 19.4" W
Presa Garabato, Tototlán	Santiago-Chapala	Grande de Santiago	12	24° 37' 28.4" N, 102° 41' 15.6" W
Joya Grande	Upper Lerma	Upper Lerma	2	20° 5' 25.3" N, 100° 32' 40.8" W
Manantial del seminario	Upper Lerma	Upper Lerma	1	21° 28' 42.2" N, 101° 15' 6.6" W
Presa Juriquilla	Upper Lerma	Upper Lerma	3	20° 41' 56.3" N, 100° 27' 31.7" W
Laguna de Almoloya	Upper Lerma	Upper Lerma	12	19° 9' 8.4" N, 99° 29' 30.6" W
Pateo-Contepec	Upper Lerma	Upper Lerma	1	19° 54' 33.1" N, 100° 19' 5.1" W
Tepuxtepec	Upper Lerma	Upper Lerma	6	19° 58' 50.1" N, 100° 14' 12.6" W
Achacales	Ayuquila	Armería	3	19° 42' 14.1" N, 104° 8' 37.9" W
El grullo	Ayuquila	Armería	2	19° 42' 16.6" N, 104° 31' 41.1" W
Atenguillo	Ayuquila	Armería	4	20° 19' 16.6" N, 104° 31' 41.1" W
Opoepo	Zirahuén	Zirahuén	3	19° 26' 12.2" N, 101° 44' 23.9" W
Río San Pedro	Mezquital	Mezquital	8	24° 18' 24" N, 104° 46' 20.38" W

index Φ_{CT} , Φ_{ST} and Φ_{SC} were also calculated using Arlequin v3.5.1.3 (Excoffier & Lischer, 2010).

To quantify genetic differences among recovered haplogroups of *G. atripinnis*, the authors estimated uncorrected *p*-distances and maximum likelihood (ML) distances according to the scenarios 2 and 3 tested for AMOVA in MEGA v7.0 (Kumar *et al.*, 2016).

2.5 | Genetic diversity and historical demography

The authors estimated levels of genetic diversity including the number of haplotypes (*H*), polymorphic sites (*S*), nucleotide diversity (π) and haplotype diversity (*h*). The levels of genetic diversity were calculated for haplogroups under scenarios 2 and 3 tested for AMOVA using Arlequin v3.5.1 (Excoffier & Lischer, 2010). Population size fluctuations through time were examined with a Coalescent Bayesian Skyline Plot (BSP) analysis (Drummond *et al.*, 2005) implemented in BEAST v1.8.1 (Drummond *et al.*, 2012). This analysis was conducted to infer the historical demography of the four genetically differentiated groups found in the haplotype network and corroborated by AMOVA. The substitution model was obtained in jModeltest v2 (Santorum *et al.*, 2014). The molecular clock was calibrated using the mutation

rate range for *cytb* estimated for teleosts of 0.76–2.2% per million years (Near & Benard, 2004; Zardoya & Doadrio, 1999) using an uncorrelated relaxed clock model for 50 million of generations and sampling every 500 generations. Convergence was assessed with Tracer v1.5 (Rambaut & Drummond, 2007), and the first 10% of the trees were discarded as burn-in.

3 | RESULTS

The authors obtained partial sequences of the mitochondrial cytochrome *b* gene (*cytb*: 1112 bp) from 318 individuals from 72 localities in 23 regions throughout central Mexico (Figure 1). In total, 1053 sites were invariable, whereas 52 were variable, 19 were singleton variable sites and 33 were parsimony informative.

3.1 | Haplotype network

The haplotype network showed geographic segregation with most of the samples southwest of the Lower Lerma region grouping together, whereas Northeast samples form a separate group (Figure 2). These

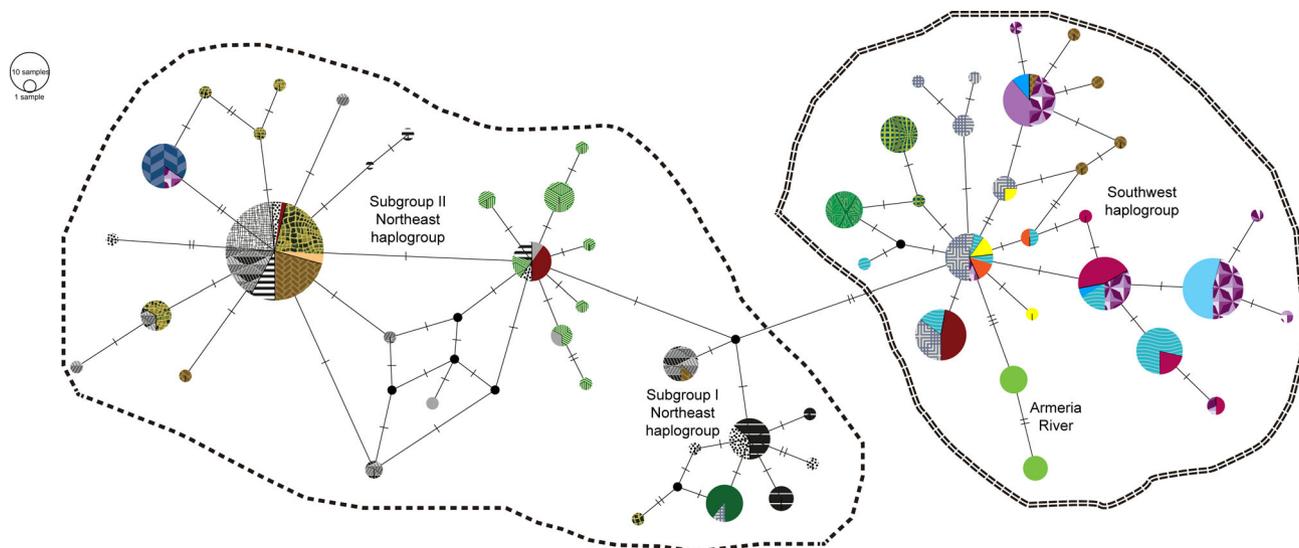


FIGURE 2 Haplotype network for all sampled populations. The size of the circles represents the relative frequency of sequences belonging to a particular haplotype (smallest circle = 1 sequence to largest circle = 63 sequences). Hatch marks along the network branches indicate the number of mutations. Each colour represents a different biogeographic region proposed by Domínguez-Domínguez *et al.* (2006) (■) MAG (■) LLE (■) AME (■) VME (■) PAN (■) AGU (■) CUI (■) VER (■) BOL (■) SMA (SAY) (■) MLE (■) CHA (■) ZAP (SAY) (■) ULE (■) PAT (■) ZAC (■) ETZ (■) JUC (■) ARM (■) COT (■) ATO (SAY) (■) BAL (■) SAY (SAY) (■) ZIR (■) MEZ (■) SAN

two geographic groups are separated by three mutational steps. Southwest haplogroup clustered the samples distributed southwest of the Lower Lerma region (Ameca, San Marcos, Zapotlán, Atotonilco, Sayula, Chapala, Etzatlán-San Marcos, Armería, Cotija and Balsas regions), with two northeastern Lerma locations (Bolaños and some samples from Cuitzeo) (Figures 2 and 3). Within this Southwest group, the Armería, Zapotlán and Sayula samples are represented by exclusive haplotypes that are separated from the nearest haplotype by three and one mutational steps, respectively. The Northeast haplogroup was comprised mainly of the samples collected in the Upper and Middle Lerma, Valley of Mexico, Pánuco, Pátzcuaro, Zacapu, Zirahuén, Juchipila, Verde, Mezquital and Aguanaval regions. The samples from the Northeast haplogroup also show geographic segregation and include two sub-groups. One sub-group is comprised mainly of samples from the Santiago (one sample), Verde, Pánuco, and all samples of Mezquital and Aguanaval regions (sub-group I). This sub-group is separated by two mutational steps from the rest of the samples within the Northeast haplogroup comprised of the remaining samples (sub-group II). The samples from Cuitzeo, Magdalena, Santiago and the Lower Lerma regions share haplotypes among the Southwest and Northeast haplogroups (Figures 2 and 3). For the case of the Lower Lerma region, samples from at least one locality (Las Adjuntas) were grouped in both geographic groups (Figure 1).

3.2 | Population structure and genetic distances

The AMOVA implemented by biogeographic regions showed molecular variance among groups of 19.09% ($\Phi_{CT} = 0.19$, $\Phi_{SC} = 0.63$ and $\Phi_{ST} = 0.70$). When the Armería River (separated by three mutational

steps of other haplotypes) was added as a third group + rest of the Southwest populations + Northeast haplogroup, the percentage of molecular variance among groups was 42.18% ($\Phi_{CT} = 0.42$, $\Phi_{SC} = 0.52$ and $\Phi_{ST} = 0.72$). Finally, when the two sub-groups within the Northeast group (separated by two mutational steps of other haplotypes) were added, the percentage of molecular variance among groups was 57.41% ($\Phi_{CT} = 0.57$, $\Phi_{SC} = 0.59$ and $\Phi_{ST} = 0.82$). In the arrangement of no *a priori* grouping, the highest percentage of variation found among populations was 67.84% ($\Phi_{ST} = 0.68$). The only comparison that was not significant was when samples were grouped according to biogeographic regions (Table 2).

The genetic distances with both implemented methods (uncorrected *p* distances and ML) were low, being 0.5% when comparing Southwest vs. Northeast populations (scenario 2) and Southwest vs. Armería River, the same value was obtained when Southwest vs sub-group II of the Northeast group (scenario 3) were compared, and of 0.7% when Armería River vs. Northeast group were compared (scenario 2) and Armería River vs. sub-group II of the Northeast group (scenario 3). The lowest genetic distance was 0.3% between Northeast sub-group I vs. Northeast sub-group II (scenario 3) (Table 3).

3.3 | Genetic diversity and historical demography

In general, the genetic diversity of *G. atripinnis* was moderate to high independent of the two group arrangements. When the genetic diversity was calculated for the two haplogroups + Armería River (scenario 2), the highest diversity was for the Southwest haplogroup ($h = 0.908$; $\pi = 0.002$; Table 4). Finally, when the four groups were considered (scenario 3), the highest genetic diversity was recovered for the

FIGURE 3 Distribution of haplotypes and haplotype diversity according to geographic location. Each colour represents a different biogeographic region according to the haplotypes network

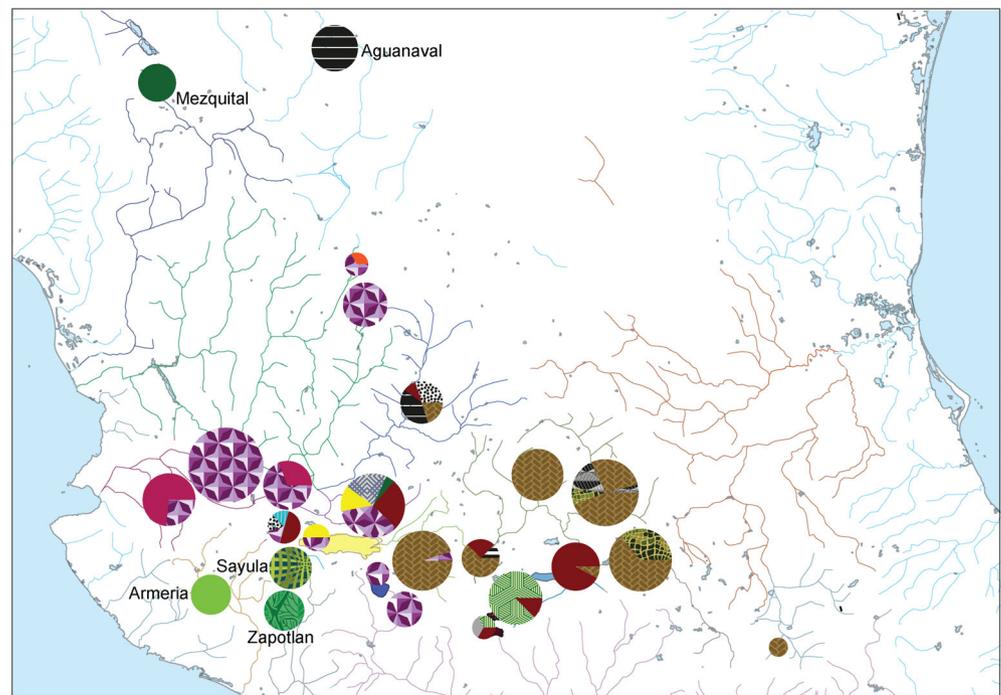


TABLE 2 Analyses of molecular variance for groups according to: (a) 23 biogeographic regions considered in the present work; (b) the two recovered haplogroups + Armería River; (c) the two sub-groups within Northeast group + Southwest group + Armería River and (d) without grouping *a priori*

Testing assumptions	Source of variation	% of variance	Fixation index
(1) Groups according to biogeographical regions	Among groups	19.09	Φ_{CT} : 0.19*
	Among populations within groups	51.19	Φ_{SC} : 0.63
	Within populations	29.71	Φ_{ST} : 0.70
	Total	100	
2) According to the two recovered haplogroups Southwest and Northeast + Armería River	Among groups	42.18	Φ_{CT} : 0.42
	Among populations within groups	30.46	Φ_{SC} : 0.52
	Within populations	27.35	Φ_{ST} : 0.72
	Total	100	
3) According to the two sub-groups within Northeast group + Southwest group + Armería River	Among groups	57.41	Φ_{CT} : 0.57
	Among populations within groups	25.39	Φ_{SC} : 0.59
	Within populations	17.20	Φ_{ST} : 0.82
	Total	100	
4) No grouping <i>a priori</i>	Among populations	67.84	Φ_{ST} : 0.68
	Within populations	32.16	
	Total	100	

An asterisk after a fixation index value is indicative of non-significance.

Southwest haplogroup ($h = 0.908$; $\pi = 0.008$), and the lowest for the Armería River ($h = 0.555$; $\pi = 0.000$; Table 4).

The BSP analysis showed that the Southwest group without the Armería population maintained a stable effective population size through time, followed by a population expansion at <0.030 Ma. When the Armería population was tested alone, this group maintained a stable effective population size through time. The sub-group I, within the Northeastern haplogroup, showed a stable effective

population size through time. Finally, for the sub-group II a constant population expansion occurred through the time (Figure 4).

4 | DISCUSSION

The results from this study, based on mitochondrial data, fail to recover significant genetic structure in *G. atripinnis* throughout most

TABLE 3 Uncorrected genetic distances/ML distances based on *cytb* within (*in italics*) and between haplogroups recovered for scenarios 2: the two haplogroups + samples of Armería River and 3: the two sub-groups for the Northeast haplogroup + Armería River + Southwest haplogroup

Scenario 2	Southwest haplogroup	Northeast haplogroup	Armería River	
Southwest haplogroup	0.003/0.003			
Northeast haplogroup	0.005/0.005	0.002/0.002		
Armería River	0.005/0.005	0.007/0.007	0.001/0.001	
Scenario 3	Southwest haplogroup	Armería River	Northeast haplogroup (sub-group I)	Northeast haplogroup (sub-group II)
Southwest haplogroup	0.003/0.003			
Armería River	0.005/0.005	0.001/0.001		
Northeast haplogroup (sub-group I)	0.004/0.004	0.006/0.006	0.002/0.002	
Northeast haplogroup (sub-group II)	0.005/0.005	0.007/0.007	0.003/0.003	0.001/0.001

cytb

Scenario 2	N	S	H	π	h
Northeast haplogroup	161	31	31	0.002 ± 0.001	0.825 ± 0.027
Southwest haplogroup	148	21	25	0.002 ± 0.001	0.908 ± 0.008
Armería River	9	2	2	0.000 ± 0.000	0.555 ± 0.090
Scenario 3	N	S	H	π	h
Sub-group I of Northeast haplogroup	28	8	7	0.001 ± 0.000	0.743 ± 0.053
Sub-group II of Northeast haplogroup	133	25	24	0.001 ± 0.000	0.754 ± 0.037
Southwest haplogroup	148	21	25	0.002 ± 0.001	0.908 ± 0.008
Armería River	9	2	2	0.000 ± 0.000	0.555 ± 0.090

TABLE 4 Genetic diversity for scenarios 2: the two recovered haplogroups + Armería River and 3: the two sub-groups within Northeast groups + Southwest group + Armería River

Note. π : nucleotide diversity; H: number of haplotypes; h: haplotype diversity; N: sample size; S: polymorphic sites.

of the currently isolated basins. This is surprising because other freshwater species in central Mexico show distinctive genetic structure across these same basins (Beltrán-López *et al.*, 2018; Domínguez-Domínguez *et al.*, 2008a, 2010; Pérez-Rodríguez *et al.*, 2009, 2015). The results presented herein show that *G. gracilis* and *G. luitpoldii* were genetically undifferentiated from *G. atripinnis*.

The results of this study revealed weak but significant phylogeographic structure, indicating the existence of four genetically differentiated groups; the sub-groups I + II within the Northeast + Southwest haplogroup + Armería River (Figures 2 and 3; Tables 2 and 3). The mtDNA phylogeographic results showed that the Northeast and Southwest haplogroups are separated by a small number of mutations, and even shared haplotypes among regions. In addition, other isolated drainages show low genetic differentiation with haplotypes not shared with other drainages, which can be explained by the lack of recent hydrological connections among drainages, as is the case of the Armería River, Sayula and Zapotlán lakes areas (Rosas-Elguera *et al.*, 1996; Rosas-Elguera & Urrutia-Fucugauchi, 1998).

A previous hypothesis proposed that *G. atripinnis* likely originated in the Santiago River, later dispersed to Lerma River at *c.* <1.7 Ma and then dispersed all along the TMVB (Domínguez-Domínguez

et al., 2010). This scenario is not supported by the results presented herein, because the haplotypes from the Santiago River (BOL and JUC) are peripheral, do not represent the central haplotype (Beheregaray & Sunnucks, 2001) and also show very low polymorphism.

4.1 | Geographic groups

The haplotype network supports the existence of two main haplogroups with low intergroup genetic distances (*p* and ML = 0.5%), separated by two mutational steps (Figure 2). These two haplogroups show geographical congruence, with one mainly distributed southwest of the Lower Lerma region and the other mainly distributed to the northeast of the Lower Lerma region (Figure 1). A similar geographic pattern has been shown in the distribution of haplotypes in plant species from the TMVB region, where clear segregation of haplotypes between east and west regions was found, indicating a lack of gene flow between these two regions (Pérez-Crespo *et al.*, 2017; Ruiz-Sanchez & Specht, 2013). This same pattern has been found in lizards and snakes (Bryson *et al.* 2011a, 2011b, 2011c, 2011d), for which genetic structure is correlated with the western, central and eastern regions of the TMVB.

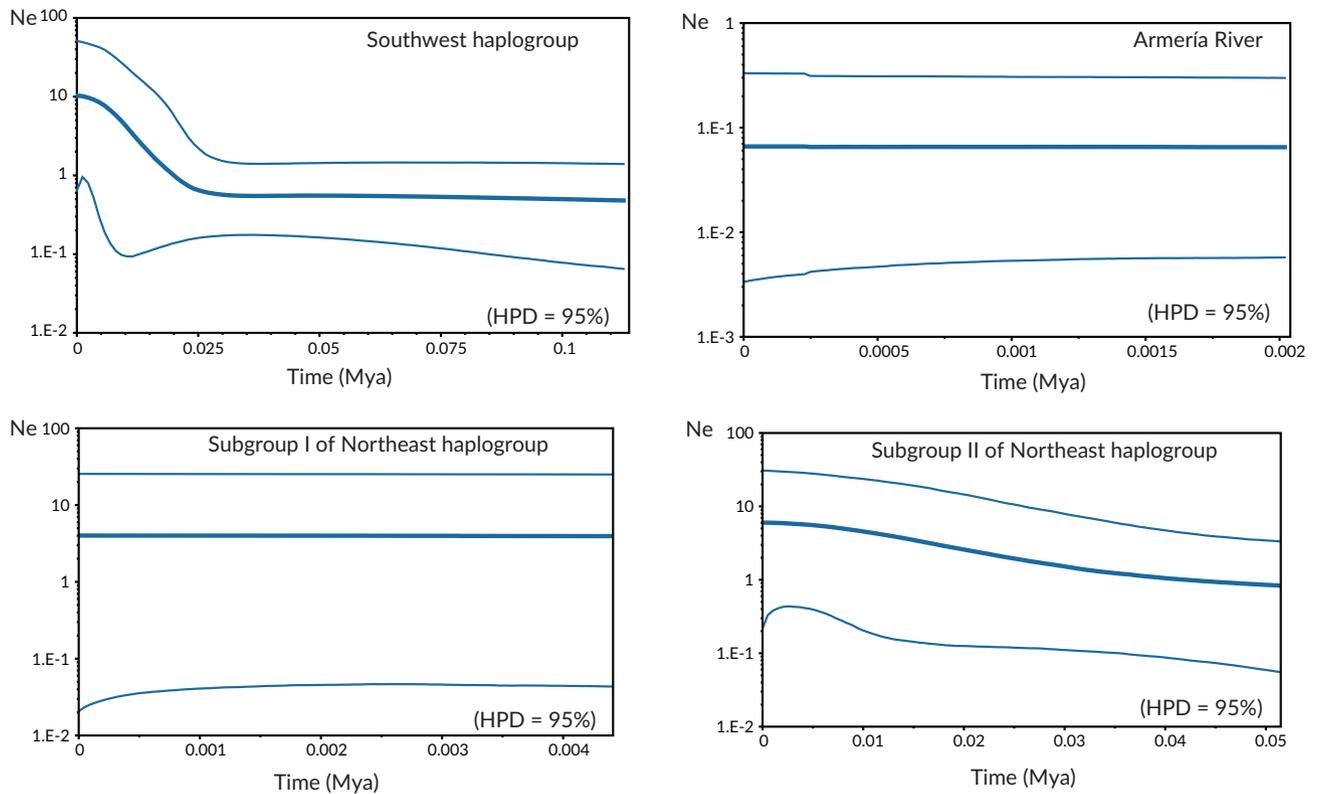


FIGURE 4 Bayesian Skyline Plots according to the four recovered groups of the haplotype network (Southwest group + Armería River + subgroup I + sub-group II of the Northeast geographic group)

The biogeographic break between northeastern and southwestern haplogroups of the Lerma River was previously found for other fish species such as *Zoogoneticus quitzeoensis* (Goodeidae) and *Allophorus robustus* (Bean 1892), but with a higher level of mean genetic distance for *cytb* ($D_p = 3.05\%$ and $D_p = 1\%$, respectively) between these two lineages (Domínguez-Domínguez *et al.* 2008a, 2008b, 2010). The differences in the genetic distance results among these two species and *G. atripinnis* could be related to the ecological and biological differences among these goodeid fishes.

Among the biological characteristics that could influence genetic differentiation is sexual selection. Within Goodeidae, there is a wide range in degree of sexual selection among species, as some species possess a strong degree of sexual selection and marked dimorphism, as is the case of *Xenotoca variata* (Bean, 1887) and *Z. quitzeoensis*, and other species with low level of sexual selection and low dimorphism, such as *G. atripinnis* (Macías-García & Valero, 2010). Previous studies, which include several species of goodeids, have established that species with strong sexual dimorphism and sexual selection showed greater degree of genetic differentiation with larger values of F_{ST} in comparison to monomorphic species with a low degree of sexual selection (Ritchie *et al.*, 2007). This could imply that for monomorphic species, as is the case of *G. atripinnis*, the weaker female-biased sexual selection has had a low influence on genetic differentiation, thus promoting homogenization. Another biological characteristic that could influence the differences between species is the high fecundity and

omnivorous feeding habits in *G. atripinnis*, contrary to *Z. quitzeoensis* and *A. robustus* that possess low fecundity and are carnivorous species (Acuña-Lara *et al.*, 2006; De la Vega-Salazar, 2006; Mercado-Silva *et al.*, 2006; Ramírez-Herrejón *et al.*, 2007; Uribe *et al.*, 2005). These differences could represent an advantage for *G. atripinnis*, allowing to establish populations in large number in habitats with different food resources as it colonized different regions.

Ecological aspects also potentially played a role in the low genetic differentiation found herein. *G. atripinnis* is highly tolerant to environmental degradation, can inhabit different aquatic habitats with different environmental conditions, is the most widespread species of fish in central Mexico drainages and is often highly abundant at sites where it occurs (De la Vega-Salazar, 2006; Domínguez-Domínguez *et al.*, 2010; Miller *et al.*, 2005; Ritchie *et al.*, 2007). All the ecological and biological aspects mentioned earlier could be related to increases or the maintenance of stable effective population sizes in *G. atripinnis* as showed by the BSP analyses (Figure 4), which in turn slow the effect of genetic drift and reduce the probability for the fixation of new mutations (Frankham, 1995; Kliman *et al.*, 2008). In contrast, *Z. quitzeoensis* and *A. robustus* are considered environmentally sensitive species, with a reduction of 25% and 33% of their historic localities, respectively. They also show low abundances relative to other goodeids and specific habitat requirements (Acuña-Lara *et al.*, 2006; De la Vega-Salazar, 2006; Mercado-Silva *et al.*, 2006; Soto-Galera *et al.*, 1999).

The aforementioned biological and ecological characteristics of *G. atripinnis* (Mendoza, 1962; Miller *et al.*, 2005; Ritchie *et al.*, 2007) could play important roles in the dispersal ability of the species. These features may have allowed *G. atripinnis* to survive and disperse through a range of habitats resulting in the low genetic differentiation among populations.

(Hartl & Clark, 1997), as has been found in other fish species (Beheregaray & Sunnucks, 2001; Croteau, 2010).

4.2 | Other divergent groups

The populations of *G. atripinnis* from the Armería River, Sayula and Zapotlán Lakes show some differentiation and do not share haplotypes with other populations (Figures 2 and 3). The Armería River population showed mean genetic distances of $D_p = 0.7\%$ and are separated by three mutational steps for the closest haplogroup (Figure 2; Table 3). A plausible explanation for this isolation pattern is a unidirectional faunal exchange because of a river capture followed by the isolation of the Armería River. This is supported by the distribution of other representative fish species of the rivers of the highlands of central Mexico (e.g., Lerma-Santiago river system) in Armería, as is the case of *Poeciliopsis infans* (Woolman 1894), *Moxostoma austrinum* Bean 1880, *Zoogoneticus purhepechus* Domínguez-Domínguez, Pérez-Rodríguez, & Doadrio, 2008 and *Ictalurus dugesii* (Bean, 1880), and the lack of representative species of the Armería River in rivers of the highlands of central Mexico (Domínguez-Domínguez *et al.*, 2010). There is evidence of river capture events promoting cladogenesis and diversification for other groups of fishes in the region, including goodeids and cyprinids (Beltrán-López *et al.*, 2017; Domínguez-Domínguez *et al.*, 2010; Pérez-Rodríguez *et al.*, 2009; Schönhuth & Doadrio, 2003).

In the case of *Goodea* from Sayula and Zapotlán Lakes, these samples do not share haplotypes with other areas (Figures 2 and 3) and are separated by one mutational step for the closest haplotypes (Figure 2). This pattern of isolation of fish fauna from these lakes also has been found for other goodeines including *Ameca splendens* Miller and Fitzsimons 1971, *Xenotoca melanosoma* Fitzsimons 1972 (Domínguez-Domínguez *et al.*, 2010) as well as the poeciliid *P. infans* (Beltrán-López *et al.*, 2018; Mateos *et al.*, 2002) with genetic distances below 0.02%. These authors suggest two alternative scenarios: (a) a recent event of faunal interchange *via* river capture or (b) a vicariant event during the formation of the current watersheds throughout the Pleistocene, when the Atotonilco–Zapotlán–Sayula Lakes were isolated, both promoted by the intense tectovolcanic activity of the so-called triple junction (Garduño-Monroy & Tibaldi, 1991).

4.3 | Recent dispersal events

The presence of *G. atripinnis* in some peripheral basins in the Atotonilco, Zacapu and Pánuco regions is similar to the distribution of other fish species such as *Z. quitzeoensis*, *Skiffia lermae* Meek 1902,

A. robustus, *X. melanosoma*, *X. variata* (Bean 1887) (Domínguez-Domínguez *et al.*, 2010), *Yuririra alta* (Jordan 1880) (Domínguez-Domínguez *et al.*, 2007), *Algansea tincella* (Valenciennes 1844) (Pérez-Rodríguez *et al.*, 2009) and *P. infans* (Beltrán-López *et al.*, 2018; Mateos *et al.*, 2002). The presence of these species in peripheral basins may be the result of river piracy events during recent geological times (less than 1 Ma). River capture is considered the main mode of dispersal that has influenced the recent evolutionary history of goodeines, at least during the last 2 Ma (Domínguez-Domínguez *et al.*, 2010). This, together with the biological and ecological characteristics of *G. atripinnis*, may explain the low genetic distances and the presence of shared haplotypes between several biogeographic regions.

One interesting result is the fact that populations of *G. atripinnis* from the Santiago River region were grouped in both main haplogroups; nonetheless, the samples collected upstream of Salto de Juanacatlán (a waterfall c. 20 m in height) were grouped in the Northeast haplogroup, whereas populations downstream of Salto de Juanacatlán were grouped in the Southwest haplogroup, indicating that the falls may act as a geographic barrier for dispersal of populations (Figure 1), as also has been found for *P. infans* (Beltrán-López *et al.*, 2018) and *M. austrinum* (Pérez-Rodríguez *et al.*, 2016).

4.4 | Human biased dispersal

Samples of *G. atripinnis* from the Valley of México, Mezquital, Magdalena and Balsas biogeographic regions showed null genetic diversity (Figure 2; Supporting Information Table TABLE S1). These drainages have a long history of isolation, and no recent natural connections to geographically proximate basins of central Mexico (Domínguez-Domínguez *et al.*, 2006, 2010). Accordingly, three possible scenarios could explain this pattern. First, the low genetic diversity could be related to recurrent population bottlenecks (Parra *et al.*, 2018); nonetheless, this scenario is not supported by the BSP results of this study that do not show a decrease in effective population size through time for any of the genetic groups analysed for *G. atripinnis* populations. Second, it has been recognized that selective pressures could be related to low genetic diversity in natural populations (Cvijovic *et al.*, 2018); nonetheless, considering that *G. atripinnis* has a high degree of ecological plasticity (Foster *et al.*, 2015) and is a monomorphic species (Ritchie *et al.*, 2007), this scenario is less probable. The final and most plausible explanation is a founder effect because of recent human-mediated dispersion (Beltrán-López *et al.*, 2018; Corona-Santiago *et al.*, 2015).

This human-mediated dispersal could be related to different sources. The introduction and translocation of species of *Chirostoma*, *Oreochromis* and *Tilapia*, which is a common and extensive practice implemented by the Mexican government (Hernández-Rodríguez *et al.*, 2001), is a plausible explanation. The data collected in this study, including the existence of shared haplotypes for Mezquital and Santiago Rivers, support this idea. Other explanations could be related to prehispanic translocations. Goodeines have long had great importance as food for indigenous populations in Mexico since their establishment 3000 years ago. Even today, these fishes are an important part of the

food supply for natives of central Mexico (Bravo-Espinosa *et al.*, 2009; Guzmán *et al.*, 2001; Parsons, 2010; Williams & Weigand, 1996). Archaeological remains of *G. atripinnis* have been found in several parts of central Mexico, reinforcing the idea that humans could have moved specimens among basins (Bravo-Espinosa *et al.*, 2009; Guzmán *et al.*, 2001), as has been explained for species of the genus *Allotoca* in Balsas river basin (Corona-Santiago *et al.*, 2015). In other cases, such as Etzatlán-San Marcos and Valley of Mexico, the lack of genetic diversity for *Goodea* could be related to the construction of irrigation channels that were built between the Etzatlán-San Marcos endorheic basin and Magdalena Lake. This is congruent with the haplotype network because the only haplotype of Etzatlán-San Marcos endorheic basin is shared with Magdalena Lake (Figures 2 and 3), whereas in the case of Valley of Mexico, an artificial connection with Pánuco contiguous basin was established since 1607, where the drainage Tajo de Nochistongo was built to drain the Valley of Mexico lacustrine area to the Tula River, in the Pánuco basin (Alcocer-Durand & Escobar-Briones, 1992). This scenario of human-mediated translocation has been proposed for other fish species in central Mexico, as *P. infans*, *Allotoca catarinae* (De Buen 1942) and *Chapalichthys encaustus* (Jordan and Snyder 1899) (Beltrán-López *et al.*, 2018; Corona-Santiago *et al.*, 2015; Galindo-Villegas & Sosa-Lima, 2002; Mar-Silva *et al.*, 2019; Ramírez-Herrejón *et al.*, 2013).

4.5 | Demographic history

The demographic history for the Southwest group, excluding the Armería population and for sub-group II of the Northeast haplogroup, shows stable effective population sizes through time with a recent population expansion at <0.030 Ma (LGM: last glacial maximum). The Armería population and sub-group I of the Northeast haplogroup possess a constant and stable effective population size through the time (Figure 4). These results contrast with the result of other analyses implemented for freshwater fishes of central Mexico, which show a demographic decline in the last 0.150–0.100 Ma (last interglacial), as is the case of *P. infans* (Beltrán-López *et al.*, 2018).

4.6 | Taxonomic implications

The taxonomy of *Goodea*, based on morphological characters, has not been consistent with three species (*G. atripinnis*, *G. luitpoldii* and *G. gracilis*) being recognized at one time or another (Doadrio & Domínguez, 2004; Domínguez-Domínguez *et al.*, 2010; Webb *et al.*, 2004). The results presented herein using mtDNA found that samples of the three recognized species included in the study share haplotypes among them (Figures 2 and 3). In this sense, it is possible that morphological differences within *G. atripinnis* be influenced by environmental factors, in which different populations show similar phenotypic responses to similar environmental gradients and water flow regimes, despite the lack of intraspecific genetic variation across their respective range. As a result, populations of *G. atripinnis* may show adaptive responses to divergent habitats, including mouth position, dorsal fin position, anal fin position and length and width

of caudal peduncle, considering that phenotypic plasticity may promote morphological adaptive response as a result of environmental changes (Foster *et al.*, 2015; Robinson & Wilson, 1994).

Other goodeids, including species of *Ilyodon*, exhibit high levels of morphological variation that do not agree with the patterns and degree of genetic variation, in which three described species clustered in the same clade in phylogenetic analyses, and shared haplotypes between recognized species (Beltrán-López *et al.*, 2017). Moreover, sympatric trophic morphs of *Ilyodon* do not show allozymic differences, concluding that the sharp trophic differences are probably a discontinuous ecophenotypic polymorphism segregating within a local population of a single biological species (Grudzien & Turner, 1984; Turner & Grosse, 1980). Other examples of deep morphological variation within species are found in the two trophic morphs of *Astyanax* that occur in sympatry in Catemaco Lake. These morphs show morphological differences in body shape and trophic traits but share haplotypes between morphs (Ornelas-García *et al.*, 2014). Despite the results of the present work, no robust taxonomic conclusion should be made from the present study because it is based on a single mitochondrial gene. The inclusion of more powerful genetic markers will be needed to make conclusive recommendations regarding the taxonomic status of three species of *Goodea*.

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AUTHOR CONTRIBUTIONS

R.G.B.L. and O.D.D. conceived the original ideas; R.G.B.L., O.D.D. and A.F.M.S. generated the data; R.G.B.L., O.D.D. and I.D. performed data analyses; R.G.B.L., O.D.D., K.R.P., H.M.M., A.F.M.S. and I.G. wrote and reviewed the manuscript; and O.D.D., K.R.P. and I.G. contributed with funding.

ORCID

Rosa Gabriela Beltrán-López  <https://orcid.org/0000-0001-8955-7603>

Omar Domínguez-Domínguez  <https://orcid.org/0000-0001-9583-4443>

Kyle R. Piller  <https://orcid.org/0000-0003-1289-9351>

Ignacio Doadrio  <https://orcid.org/0000-0003-4863-9711>

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