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RESEARCH ARTICLE

Biotic regionalization of freshwater fishes in Northern Middle America highlights high beta diversity created by prominent biogeographic barriers

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Abstract

Northern Middle America (NoMA) is considered a transition zone between the Nearctic and Neotropical biogeographic realms. In this region, Nearctic and Neotropical freshwater fishes create regional faunas of mixed origin, but their general biogeographic patterns have not been quantified. To identify such patterns, we delineate biogeographic regions (BRs) and major biogeographic barriers of NoMA and summarize patterns of faunal similarity among BRs. We used clustering analysis on a presence-absence matrix of primary and secondary freshwater fishes to group 97 level-6 HydroBASINs units spanning NoMA into BRs. We assessed statistical support of clusters using one-way analysis of similarity and implemented a species-indicator analysis. We delineated biogeographic barriers with the software Barrier 2.2 and determined faunal similarity among BRs using beta diversity-Jaccard dissimilarity and producing a minimum-spanning tree. Seven statistically distinctive and geographically coherent BRs were delineated and described. Barrier analysis identified three major barriers within NoMA. The first barrier combines the Sea of Cortés (Gulf of California) and Sierra de Juárez-Cerro Gordo highlands. The second combines the Trans-Mexican Volcanic Belt, Sierra Madre del Sur, and Sierra Madre de Chiapas highlands. The third combines the Río Grande Rift, Sierra Madre Occidental, and Mesa Central highlands. Faunal dissimilarity was very high among BRs, with lowest dissimilarity (92%) between the Balsas-Nacaome and Grijalva-Usumacinta BRs. Boundaries of NoMA BRs do not correspond with political boundaries. We concluded that bioregions of NoMA are faunally distinct, with limited overlap due to presence of strong, long-standing geographical barriers enhanced by aridity in the North.

Highlights

- Seven distinct and geographically coherent bioregions were detected in Northern Middle America based on obligate freshwater fishes.

- Biotic regionalization of Northern Middle America is greatly influenced by the presence of three biogeographic barriers: (1) the Sea of Cortés and Sierra de Juárez-Cerro Gordo highlands; (2) the Trans-Mexican Volcanic Belt, Sierra Madre del Sur, and Sierra Madre de Chiapas highlands; and (3) the Río Grande Rift, Sierra Madre Occidental, and Mesa Central highlands.

- Species richness across bioregions in Middle America vary from two species in Baja California to 187 in the Grande-Pánuco. Dissimilarity among bioregions ranged from 0.92 to 0.98%, excluding the Baja California bioregion which was 100% different from all other bioregions. Such levels of faunal distinctiveness suggest the presence of strong, long-standing geographical barriers enhanced by aridity in the North.

- Our results suggest that the northern boundary of Middle America is not delimited by the political border between the USA and Mexico. Instead, the biological northern border of Middle America extends into the USA drainages in California, the Colorado River basin and the headwaters of the Río Grande in the Southern Rocky Mountains.

Keywords: dispersal, biogeographic barriers, Mexico, Central America, UPGMA, bioregions

Introduction

Classification of the Earth's surface into biogeographical regions (BR from here on) based on patterns of distribution is a central goal in biogeography (Ficetola et al. 2017, Kreft and Jetz 2010, Smith et al. 2020, Alahuhta and García-Girón 2022). A BR contains a characteristic set of taxa (Escalante 2009, Ennen et al. 2017, Ennen et al. 2020), and boundaries between BRs represent locations of faunal turnover (i.e., change in the unique set of taxa within a geographic region) (Ennen et al. 2020, Matamoros et al. 2016, Smith and Bermingham 2005). Biogeographic regions reflect biogeographical legacies that shaped species distributions (Hansen et al. 2021), including historical (Lomolino et al. 2010) and ecological (e.g., niche parameters, biological interactions; Ricklefs, 1987) aspects. Delimitation of BRs provides a framework for understanding the geography of biodiversity (e.g., Matamoros et al. 2012, 2015, 2016, Ennen et al. 2017, 2021), which is central for conservation (Ennen et al. 2020).

Northern Middle America (NoMA) is a transition zone between the Nearctic and Neotropical biogeographic realms where freshwater fishes from the Nearctic and the Neotropics intermingle, creating regional faunas of mixed origin. Despite having unique fish assemblages, general biogeographic patterns have not been quantified in NoMa inclusive of Mexico. In a comprehensive, but qualitative study, Miller et al. (2005) divided Mexico into eight BRs. However, these authors truncated the boundaries of their BRs at political borders, which are not necessarily biogeographical boundaries. Later, Abell et al. (2008) proposed ~29 BRs in NoMA. Their designation was also qualitative. In a global study, Leroy et al. (2019) identified NoMA as a transition zone between Nearctic and Neotropical regions and they detected large-scale biogeographic substructure in the Nearctic and Neotropical sections of NoMA (Leroy et al. 2019, supporting information 7.13-14), but they did not identify fine-scale substructure.

Recently, freshwater bioregions were proposed based on obligate freshwater fishes (primary and secondary *sensu* Myers, 1949) using quantitative approaches for Central America (Matamoros et al., 2015) and for the contiguous USA (Matamoros et al. 2016), lying south and north of NoMA, respectively. Studies in Central America and southern Mexico (Matamoros et al., 2015) indicate that the southern Mexican BRs of Miller et al. (2005) do not stop at the international boundary, but extend into Guatemala on the Caribbean slope and Honduras on the Pacific slope (Matamoros et al., 2015). On the other hand, BRs of the USA were truncated at the Mexico border (Matamoros et al. 2016), so their extension into NoMA is unknown.

Herein, we present a quantitative bioregionalization of NoMA based on continental ichthyofauna. We first identify the number of BRs present based on clustering analysis with level-6 HydroBASINs as analytical units. We then delineate major biogeographic barriers. Finally, we summarize patterns of faunal similarity among BRs. All analyses include HydroBASINs within Central America that are known to have affiliation with Mexican HydroBASINs (Matamoros et al., 2015). Further, analysis included bordering BRs within the USA to allow for identification of international BRs.

Materials & Methods

Study area and distributional data

We defined NoMA as the region between the Motagua Fault, Guatemala and Mexico (Elías et al. 2020) and the Southwestern Plains, Colorado River Basin, and California biogeographic provinces, USA (Matamoros et al. 2016) (Fig. 1, Table S1). Our sampling unit was level-6 HydroBASINs (global HydroBASINs dataset, Linke et al. 2019) (*sensu* Ennen et al. 2020, 2021). We generated a presence-absence (1-0) data matrix using obligate freshwater fish species across the 97 level-6 HydroBASINs units spanning NoMA (Fig. 1). The fish fauna of NoMA is well known (e.g., Moyle 2002, Miller et al. 2005, Minckley and Marsh 2009), but to be thorough, distributional data were obtained through literature searches, online aggregators [Global Biodiversity Information Facility (GBIF; http://www.gbif.org, last accessed in August 2021) and FishNet 2 (http://www.fishnet2.net, last accessed in August 2021)], and with internet queries filtered to include only georeferenced museum specimens from Mexico, Belize, and Guatemala. After curating the dataset to avoid duplicate entries, the final presence-absence matrix consisted of 499 recognized species, representing 135 genera and 23 families (Table S1). Taxonomic nomenclature was standardized using Eschmeyer's Catalog of Fishes (Fricke et al. 2020).

Biogeographic regionalization

To determine the number of BRs in NoMA, we first generated a dendrogram describing faunal relationships among HydroBASINs. We used the unweighted pair group with arithmetic mean (UPGMA) method, which has robust performance in analysis of large-scale datasets (Kreft and Jetz 2010, Ennen et al. 2020) and has been successfully used in other studies of freshwater fish bioregionalization (e.g., Smith & Bermingham, 2005; Matamoros et al., 2012, 2015, 2016; Elías et al., 2020). We implemented the UPGMA with a distance matrix using the beta diversity-Jaccard dissimilarity index (β_{jac}) (Baselga 2010, Baselga 2012). Subsequently, a cophenetic correlation coefficient (Farris 1969) was used to estimate the goodness of fit of the UPGMA by calculating the correlation between the original matrix and the resulting distance matrix. Coefficients > 0.9 indicate very good fit, coefficients between 0.8 and 0.9 indicate good fit, and coefficients < 0.8 indicate poor fit (Rohlf 1997). To identify the optimal number of groups (i.e., BRs) present in the UPGMA, we used the Kelley-Gardner-Sutcliff (KGS) penalty procedure (Kelley et al. 1996), which maximizes differences among all groups in a dendrogram, while preserving homogeneity among groups (Ennen et al. 2020). After having established the optimal number

Figure 1. Map of the study area showing the 97 level-6 HydroBASINs units spanning northern Middle America (NoMA). Numbers on each drainage are coded with Table S1.

of HydroBASINs clusters (i.e., BRs) in the UPGMA, we tested if clusters were statistically distinct using one-way analysis of similarity (ANOSIM, Clarke & Warwick, 1994).

Subsequently, we used an indicator-species analysis (ISA) to determine which species characterized each BR (Dufrêne and Legendre 1997). Higher ISA values (> 0.75) occur when species occupy all or most of the HydroBASINs in a BR but are absent from all or most HydroBASINs of other BRs. In contrast, lower ISA values are observed when species are widely distributed across HydroBASINs within multiple BRs or have small ranges within a BR.

Biogeographic barriers

To delineate major biogeographic barriers, we used the software Barrier 2.2 (Manni et al. 2004), which uses the Monmonier algorithm (Monmonier 1973) designed to find the edges associated with the largest rate of change in a measure of distance (Manni et al. 2004). For this procedure, we used two input files: 1) geographic coordinates of locations (centroids of HydroBASINs, Table S2) and 2) statistical distances between HydroBASINs (i.e., beta diversity-Jaccard

dissimilarity index). The algorithm was applied to a geometric network that connects all BRs using Delaunay triangulation (Brassel and Reif 1979) and the final result was presented in a geographic map. Major barriers indicate the presence of abrupt changes in assemblage structure (Manni et al. 2004, Patten and Smith-Patten 2008).

Faunal contrasts

We calculated species richness (total species count) and beta diversity-Jaccard dissimilarity (β_{jac}; Baselga 2012) to illustrate faunal distinctiveness among BRs. To link adjacent provinces according to their faunal similarity, we built a minimum-spanning tree (Gower & Ross, 1969), which connects all BRs in the manner in which the sum of the edge lengths along the tree is minimized (Legendre and Legendre 2012). The minimum-spanning tree was implemented with a Jaccard dissimilarity index (β_{jac}), based on a presence-absence matrix of all taxa belonging to each bioregion (Table S3). For descriptive purposes, we also calculated species relative richness, dividing the species richness of each family by the total species of each BR. This

provided an estimate of the family relative richness contribution to the region.

Software

The ANOSIM procedure was performed in Past v.4.0 (Hammer et al. 2001). All other analyses, were carried out in R 4.0.5 (R Development Core Team 2021) with the following packages: vegan (Oksanen et al. 2019), betapart (Baselga et al. 2018), maptree (White and Gramacy 2012), indicspecies (De Cáceres et al. 2022) and ade4 (Thioulouse et al. 2018). Maps were created in ArcMap v. 10.6.1 (ESRI, Redlands, CA, USA).

Results

Biogeographic regionalization

The optimal solution in the clustering dendrogram recognized seven distinct BRs (k = 7 HydroBASINs clusters; Fig. 2a-b). A cophenetic correlation coefficient of 0.90 indicated very good fit to the data (see methods). All individual HydroBASINs clusters were significantly distinct (ANOSIM, P = 0.0001, R = 0.912,). Geographically, no HydroBASINs were orphans (i.e., not grouped to any cluster). Furthermore, all HydroBASINs within any cluster were geographically contiguous with others of the same cluster, indicating geographic as well as faunal coherence (Fig. 2a-b). Each HydroBASINs cluster extends from a long branch off the base of the dendrogram, deeply differentiated from all other clusters (Fig. 2a). As expected, BR boundaries did not correspond to international borders. Four BRs spanned the USA-Mexico border, one spanned the Mexico-Guatemala border, and another included parts of Mexico, Guatemala, and Belize (Fig. 2b).

Biogeographic barriers

Barrier analysis detected three biogeographic barriers that largely explained BR geography in NoMA (Fig. 3a-b). One barrier coincides with the Sea of Cortés (Gulf of California), from the northern Gulf extending westward across Baja California around the northern tip of Sierra de Juárez, continuing west to the Pacific on the northern side of Cerro Gordo (Fig. 3). This barrier isolates the Baja California BR from adjacent California and Colorado BRs.

A second barrier incorporates the western edge of the Río Grande Rift, eastern crest of the Sierra Madre Occidental, and eastern front of the Mesa Central. This barrier divides BRs on the Gulf of Mexico slope from those on the Pacific slope. However, the Sonora-Lerma BR transgresses this barrier from the west where it incorporates interior HydroBASINs on the Mesa del Norte (Fig. 3, discussed further below).

Figure 2. (a) Results of the UPGMA clustering analysis based on 499 species of obligate freshwater fishes present in 97 level-6 HydroBASINs, showing seven clusters that form distinct biogeographic regions (BRs). The red bar at the right of the dendrogram denotes Nearctic BRs and green bar grouping the Neotropical BRs. (b) Color-coded map of Northern Middle America showing the inferred seven BRs = Baja California (BC), California (Ca), Colorado (Co), Sonora-Lerma (SL), Balsas-Nacaome (BN), Grande-Pánuco (GP) and Grijalva-Usumacinta (GU).
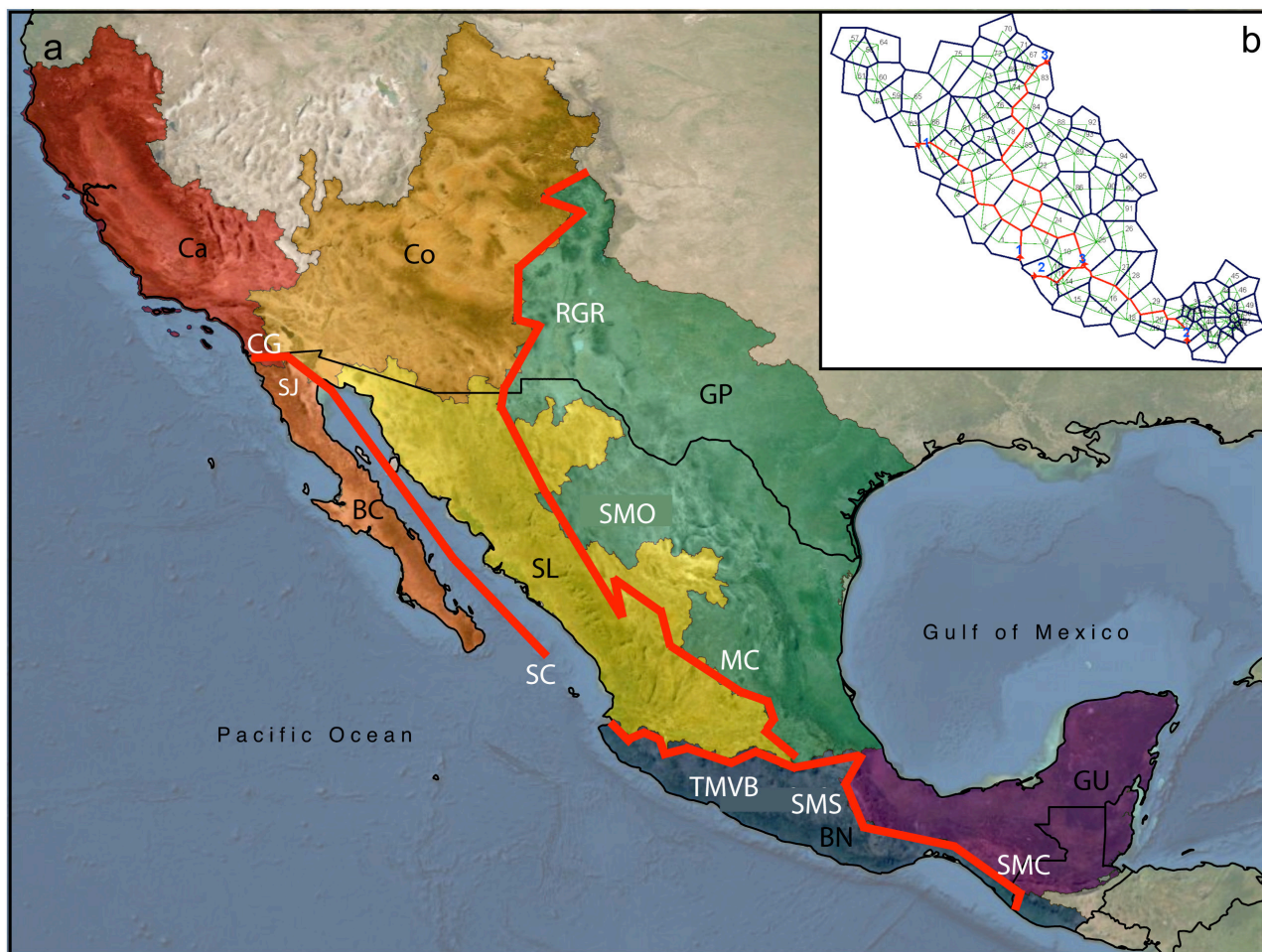
Figure 3. (a) Major geographic barriers for obligate freshwater fish in Northern Middle America as recovered by the software Barrier 2.2 (Manni et al., 2004). There are three barriers (mapped in red). One combines the Sea of Cortés (SC), Sierra de Juárez (SJ), and Cerro Gordo (CG). Another combines the Río Grande Rift (RGR), Sierra Madre Occidental (SMO), and the Mesa Central (MC). The last combines the Trans-Mexican Volcanic Belt (TMVB), Sierra Madre del Sur (SMS), and Sierra Madre de Chiapas (SMC). Bioregions are labeled in black font: California (Ca), Colorado (Co), Baja California (BC), Sonora-Lerma (SL), Balsas-Nacaome (BN), Grande-Pánuco (GP), and Grijalva-Usumacinta (GU). (b) Voronoi tessellation (polygons) and the corresponding Delaunay triangulation (internal triangles) based on sampling locations in this study showing three computed barriers based on distributions of obligate freshwater fish.

A third barrier combines the crests of the Trans-Mexican Volcanic Belt, Sierra Madre del Sur, and Sierra Madre de Chiapas. The Trans-Mexican Volcanic Belt portion of this barrier separates Neotropical BRs (Balsas-Nacaome, Grijalva-Usumacinta) from those to the north. The Sierra Madre del Sur-Sierra Madre de Chiapas portion separates the Neotropical BRs from each other on the Pacific and Atlantic (Gulf of Mexico and Caribbean) slopes (Fig. 3).

Faunal contrasts

Faunas of BRs varied in species richness, ranging from 2 to 187 species, and BRs shared few species, with faunal dissimilarity exceeding 92% in all cases (Table 1). The minimum-spanning tree illustrates highest faunal distinctiveness for the Baja California, California, and Colorado BRs (Fig. 4), which each had > 95% dissimilarity compared with all other BRs (Table 1). The four remaining BRs were organized into

pairs of neighboring BRs with faunal dissimilarity of 94% (Sonora-Lerma and Grande-Pánuco) and 92% (Grijalva-Usumacinta and Balsas-Nacaome).

Biogeographic Region (BR) descriptions

Baja California (BC) Biogeographic Region (BR)

The Baja California BR incorporates six HydroBASINs of peninsular Baja California, extending from Río Guadalupe in the north to Río San Juan del Cabo in the south (Fig. 3). Nearly all of the peninsula is arid hot desert (Peel et al. 2007) and the Baja California BR is inhabited by just two obligate freshwater species in one family: *Fundulus lima* Vaillant 1894 and *F. parvipinnis* Girard 1854, both of which are indicator species (Table S4).

California (Ca) Biogeographic Region (BR)

The California BR (Northwest-Intermountain region of Matamoros et al., 2016) extends along the Pacific

Slope from the Klamath River in the north to the Río Tijuana in the south (Fig. 3). The climate transitions from cold with dry and hot summers in the northeast to arid hot desert in the southeast (Peel et al. 2007). Twenty-nine species inhabit this BR, the most speciose families being Leuciscidae and Catostomidae (Table 2). *Catostomus occidentalis*, *Lavinia symmetricus*, *Orthodon microlepidotus*, and *Ptychocheilus grandis* are indicator species (Table S4).

Colorado (Co) Biogeographic Region (BR)

The Colorado BR (Lower Colorado region of Matamoros et al., 2016) corresponds to the Colorado River basin (Fig 3). The climate transitions from cold with dry and hot summers in the Rocky Mountains to arid hot desert at the Colorado River mouth at the head of the Sea of Cortés (Peel et al. 2007). Thirty-four species inhabit the Colorado BR, including a predominance of the families Leuciscidae and Catostomidae (Table 2). *Ptychocheilus lucius*, *Xyrauchen texanus*, *Catostomus latipinnis*, *Gila elegans*,

Gila robusta, *Pantosteus discobolus*, and *Gila cypha* are indicator species (Table S4).

Grande-Pánuco (GP) Biogeographic Region (BR)

The Grande-Pánuco BR (expansion of the southern plains bioregion *sensu* Matamoros et al., 2016) extends along the Gulf of Mexico slope from the Colorado River (Texas) on the north to Río Nautla on the south (Fig. 3). Inland, it extends from the headwaters of the Río Grande in the Southern Rocky Mountains and Río Grande Rift of the Chihuahuan Desert. The climate transitions from temperate with no dry season and hot summers in the northeast to temperate with no dry season and cold summers in the southeast, but there is much climatic variation throughout, including areas of arid hot desert and others with a tropical monsoon climate (Peel et al. 2007). The Grande-Pánuco is the largest BR by area and has the highest species richness, with 187 species. Taxa from the families Leuciscidae and Poeciliidae are most numerous (Table 2). *Cyprinella lutrensis*, *Pylodictis olivaris*, *Gambusia affinis*, and *Ictalurus punctatus* are indicator species (Table S4).

Sonora-Lerma (SL) Biogeographic Region (BR)

The Sonora-Lerma BR includes HydroBASINs of the Mexican Pacific slope and select interior HydroBASINs within the Mesa del Norte (Fig. 3) from Río Sonoyta in the north to Río Ameca in the south. The eastern boundary, however, imperfectly conforms with the Río Grande Rift-Sierra Madre Occidental-Mesa Central barrier because the Cuencas Cerradas Norte and Nazas Aguanaval HydroBASINs units (numbers 24 and 27, Fig. 1) are included. The climate of the Sonora-Lerma BR transitions from arid hot desert in the northwest to tropical savannah in the southwest (Peel et al. 2007). Eighty-six species inhabit the Sonora-Lerma BR, with Leuciscidae and Goodeidae as the most numerous families (Table 2). *Campostoma ornatum* and *Mayaheros beani* are indicator species (Table S4).

Balsas-Nacaome (BN) Biogeographic Region (BR)

The Balsas-Nacaome BR is on the Pacific slope, extending south and west from the Jalisco Coast (several small rivers) to the coasts of Chiapas and Guatemala (Fig. 3). The climate transitions from temperate with no dry season and cold summers in the northeast to tropical rainforest in the southeast (Peel et al. 2007). Sixty-seven species inhabit the
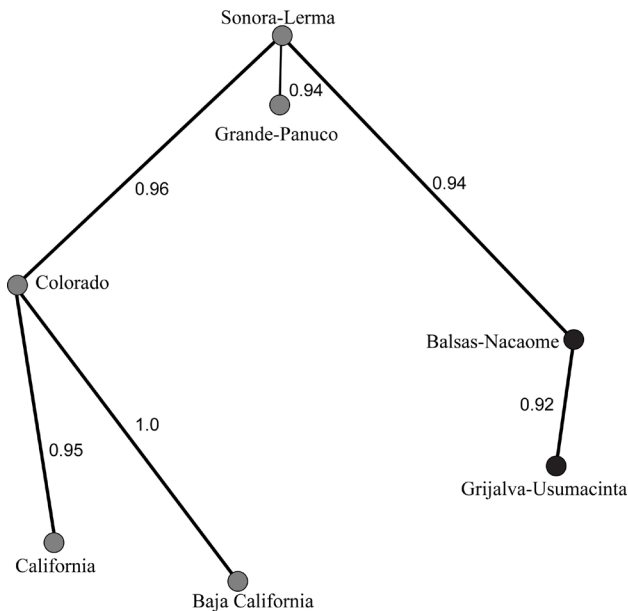

Figure 4. Minimum spanning tree (MST) among bioregions (BRs). Computed from the beta diversity-Jaccard dissimilarity coefficient among bioregions. Bold dots represent Nearctic BRs and gray dots Neotropical BRs.

Table 1. Pairwise beta diversity-Jaccard dissimilarity among biogeographic regions (BRs). Species richness of each BR is given in parenthesis with region names.

BR	SL	BN	GP	GU	Ca	Co
Baja California (BC) (2)	1.00	1.00	1.00	1.00	1.00	1.00
Sonora-Lerma (SL) (86)	0	0.94	0.94	1.00	1.00	0.96
Balsas-Nacaome (BN) (67)		0	0.98	0.92	1.00	1.00
Grande-Panuco (GP) (187)			0	0.97	1.00	0.96
Grijalva-Usumacinta (GU) (155)				0	1.00	1.00
California (Ca) (29)					0	0.95
Colorado (Co) (34)						0

Table 2. Species richness of obligate freshwater fishes by family and biogeographic region (BR). BRs are ordered left to right by percent contribution of Neotropical families (abbreviations follow Table 1). Nearctic families (toward top of table, dark-gray rows, white text) are ordered top to bottom by how far to the right on the table each family is distributed. Similarly, Neotropical families (toward bottom of table, light-gray rows, black text) are ordered bottom to top by how far to the left on the table each family is distributed. BRs abbreviations: BC= Baja California, Ca= California, Co= Colorado, SL= Sonora-Lerma, GP= Grande-Pánuco, BN= Balsas-Nacaome, GU= Grijalva-Usumacinta

Family	BC	Ca	Co	SL	GP	BN	GU
Cottidae		1					
Amiidae					1		
Lepisosteidae					2		
Percidae					4		
Centrarchidae		1			13		
Goodeidae		1		21	3	17	
Fundulidae	2				7		3
Catostomidae		10	7	10	19		2
Cyprinodontidae		4	3	6	16		12
Ictaluridae				2	11	1	1
Leuciscidae		12	23	32	58	6	1
Poeciliidae			1	12	37	18	57
Characidae				1	7	7	16
Cichlidae				2	9	8	45
Heptapteridae						2	4
Profundulidae						4	5
Synbranchidae						2	3
Anablepidae						1	
Gymnotidae						1	
Bryconidae							1
Dinematichthyidae							1
Lacantuniidae							1
Rivulidae							3
Total species	2	29	34	86	187	67	155
Percent Neotropical	0	0	2.9	17.4	28.3	64.2	87.7

Balsas-Nacaome BR, including numerous Goodeidae and Poeciliidae (Table 2). *Poecilia nelsoni*, *Poeciliopsis turrubarensis*, and *Amphilophus trimaculatum* are indicator species (Table S4).

Grijalva-Usumacinta (GU) Biogeographic Region (BR)

Located on the Gulf of Mexico-Caribbean slope, the Grijalva-Usumacinta BR (Grijalva-Usumacinta region of Matamoros et al., 2015 and Elías et al., 2020) extends from the Trans-Mexican Volcanic Belt in the north (Río La Antigua) to the Motagua-Polochic Fault Zone in the south (Río Cahabón-Polochic), encompassing the Península de Yucatán (Fig. 3). The climate transitions from temperate with no dry season and cold summers in the northeast to tropical rainforest in the southeast (Peel et al. 2007). With 155 species, the Grijalva-Usumacinta is the second most speciose BR in NoMA, with numerous species of Poeciliidae and Cichlidae (Table 2). Indicator species are *Pseudoxiphophorus bimaculatus*, *Trichromis salvini*, *Poecilia mexicana*,

Rocio octofasciata, *Cribroheros robertsoni*, *Xiphophorus maculatus*, *Rhamdia guatemalensis*, and *Thorichthys meeki* (Table S4).

Biogeographical transition among Biogeographic Regions (BRs)

A summary of distributions of Nearctic and Neotropical families (Table 2) illustrates that the seven BRs of NoMA represent a transition between realms. While some representatives of Nearctic families are found throughout the region, this decreases from 100% of species richness in the Baja California and California BRs to 35.8% in the Balsas-Nacaome BR and 12.3% in the Grijalva-Usumacinta BR. In contrast, Neotropical families are less than one third of the faunas in the Grande-Grande-Pánuco and Sonora-Lerma BRs, with just one Neotropical species found north or west of these BRs.

Discussion

Honing boundaries of Biogeographic Regions (BRs)

Although most of the BRs delineated here are well established, the Grijalva-Usumacinta BR has been redefined several times since first proposed by Miller (1966) as extending from Río Papaloapan on the north to Río Polochic on the south. Matamoros et al. (2015) found that the Río Cahabón-Polochic did not group with the remainder of the BR, causing them to propose it as a separate region. However, Elías et al. (2020) included more detailed distributional data and included the Río Cahabón-Polochic within the Grijalva-Usumacinta BR, consistent with the findings of the present study. Thus, the only difference in our present findings from Miller's (1966) original designation is our inclusion of La Antigua and Blanco rivers north of Río Papaloapan.

Similarly, the boundaries of the Balsas-Nacaome BR have been redefined several times. Miller (1966) proposed it extended from Río Tehuantepec to the Nicoya Peninsula. Matamoros et al. (2015) truncated the Balsas-Nacaome BR to only extend south as far as Río Nacaome in Honduras. Our study supports the latter. In addition, our analysis greatly expands the Balsas-Nacaome BR northward to include the extensive Río Balsas and adjacent coastal HydroBASINs to the north and west as far as Cabo Corrientes.

Barrier formation and Biogeographic Regions (BRs)

The NoMA region has a long history of active tectonism (Gray et al. 2021). Tectonic evolution has dramatically influenced river-drainage geography (described further below). As a result, it is no surprise that major tectonic features form strong biogeographic barriers for obligate freshwater fishes. The Mar de Cortés (Gulf of California) is composed of a series of drowned rift basins that opened within the last 20 Ma (Ferrari et al. 2018). The basins began to flood ~7 Ma and the Sea reached its full extent 6.3-6.5 Ma (Umhoefer et al. 2018). In addition, the climate of western North America became increasingly arid in the Middle-Late Miocene (Eronen et al. 2012, Pound et al. 2012), isolating shrunken river drainages. This combination of peninsular isolation and a scarcity of aquatic habitats created extreme isolation of Baja California BR freshwater fishes, and there is no evidence of freshwater dispersal onto or across the peninsula, which lacks a peninsular-scale river. Rather, native freshwater fishes are derived from marine forms that produced freshwater populations (Ruiz-Campos et al. 2002), which inhabit isolated oases of localized stream systems. For example, the indicator species *F. parvipinnis* occupies coastal habitats where its distribution expands and contracts in response to sea-level fluctuation (Dolby et al. 2018). The indicator species *F. lima* descends from a common ancestor with *F. parvipinnis* (Ghedotti and Davis 2017), suggesting it also has a history of coastal dispersal.

Formation of the Río Grande Rift had major implications for river-drainage geography and shifted the continental divide eastward to its modern location (Galloway et al. 2011, Snedden et al. 2018). Thereafter, it was a barrier to freshwater fishes. The Río Grande Rift initiated ~25 Ma, with active rifting over the next 10-15 Ma (Abbey and Niemi 2019). It isolates the Colorado River (Colorado BR) from the Gulf of Mexico slope. The southernmost basins of the Río Grande Rift meld with the northeastern front of the Sierra Madre Occidental, and barrier analysis indicates this is a contiguous barrier to freshwater fishes. Volcanism was widespread throughout the Sierra Madre Occidental through the Neogene (23.0-2.6 Ma) (Ferrari et al. 2018) and rivers steepened over this time as the Sierra Madre Occidental and Mesa Central uplifted (Stephenson et al. 2014). Increasing relief presumably reduced potential for east-to-west, cross-divide range expansion, especially for lowland fishes, increasing isolation of the Sonora-Lerma BR from the Grande-Pánuco BR. This barrier appears to have limited the distributions of Neotropical families, with relatively few species present west of the boundary in the Sonora-Lerma BR (Table 2).

The Trans-Mexican Volcanic Belt is a complex geological region (Gómez-Tuena et al. 2007) that developed in stages, beginning 19 Ma (Ferrari et al. 2012). For obligate freshwater fishes, this belt appears to form the main boundary between Nearctic faunas to the north and Neotropical faunas to the south, with Nearctic fishes forming the bulk of species richness on the north and Neotropical fishes from the bulk of species richness to the south (Table 2), despite substantial crossing of this barrier in both directions. Our analysis indicates the Trans-Mexican Volcanic Belt barrier is contiguous with a barrier extending southeast via the Sierra Madre del Sur and Sierra Madre de Chiapas. These uplifts also have ancient histories, with Sierra Madre del Sur forming via intense magmatism 40-28 Ma (Morán-Zenteno et al. 2018) and Sierra Madre de Chiapas uplifting 14-7 Ma (Villagómez and Pindell 2020). These mountain ranges combine to form the crest of the continental divide southeast of the Trans-Mexican Volcanic Belt, separating the Gulf of Mexico-Caribbean slope from the Pacific slope, accounting for biogeographic separation between the Balsas-Nacaome and Grijalva-Usumacinta BRs.

Faunal Similarity among Biogeographic Regions (BRs)

High distinctiveness of BR faunas and discrete separation of HydroBASINs among BRs is to be expected because regional and local endemism are prominent features within NoMA (Tisseuil et al. 2013, Griffiths 2022). For example, native fish assemblages in the desert region north of the Trans-Mexican Volcanic Belt are highly organized into areas of endemism, with a very small proportion of lineages distributed among two or more areas (Hoagstrom et al. 2020). This reflects the manner in which mountain ranges and deserts effectively fragment aquatic habitats. Fragmentation due to aridity is less pronounced south of the Trans-Mexican Volcanic Belt, but widespread tectonism has created a rugged landscape in which inter-drainage dispersal is limited.

Despite the role of the Sierra Madre Occidental as a biogeographic barrier to lowland species, the small number of species shared between the neighboring

Grande-Pánuco (Atlantic) and Sonora-Lerma (Pacific) BRs reflect colonization events across this mountain range. Examples of highland species with ranges spanning the continental divide include *Campostoma ornatum* (Domínguez-Domínguez et al. 2011), *Codoma ornata* (Schönhuth et al., 2015), *Pantosteus plebeius-nebuliferus* (Corona-Santiago et al., 2018), and Mexican trout *Oncorhynchus* spp. (Abadía-Cardoso et al. 2015). In this tectonically active region, there are also cases of river captures that produce disjunct populations across the divide from the main range of species, as in *Gila pulchra* (Schönhuth et al. 2014) and *Cyprinodon albivelis* (Hoagstrom and Osborne 2021). This phenomenon, along with endemism of lowland species, explains why the Cuencas Cerradas Norte and Nazas Aguanaval HydroBASINs units (numbers 24 and 27in Fig. 1) are included in the Sonora-Lerma BR.

In contrast, very low similarity of faunas among the Baja California, California, and Colorado BRs reflects strong isolation from each other, in contrast to high faunal overlap present among BRs of central and eastern North America (Matamoros et al. 2016). A combination of high levels of tectonic disturbance with a harsh and fluctuating climate likely accounts for low faunal richness and high faunal uniqueness within each region (Moyle and Herbold 1987, Smith et al. 2002). The freshwater fauna of the Baja California BR appears to have no past connection to any other NoMA BR (Ruiz-Campos et al. 2002), whereas the faunas of the California and Colorado BRs are primarily derived from farther north (Smith et al. 2002).

A history of extreme isolation is exemplified in the Colorado BR, which is dominated by endemic lineages (Minckley et al. 1986, Spencer et al. 2008, Hoagstrom et al. 2020). Most fishes in the Colorado BR are from Nearctic lineages and very few lineages from other NoMA provinces colonized this BR from the south. In the one exception, *Poeciliopsis occidentalis* a largely Neotropical genus (Mateos et al. 2019), occupying southeastern portions of the Colorado BR (Miller et al., 2005), likely due to an inter-drainage stream exchange from the Sonora-Lerma BR.

In addition to sharing a Neotropical climate, limited species sharing between the Grijalva-Usumacinta and Balsas-Nacaome BRs may be attributable to a history of stream exchanges. In particular, small Pacific-slope rivers south from Río Tehuantepec are generally depauperate, but include examples of fishes reaching the Balsas-Nacaome BR from Gulf of Mexico and Caribbean drainages of the Grijalva-Usumacinta BR (Bussing 1976, Miller et al. 2005). The faunas of Ríos Armería and Balsas in the northern Balsas-Nacaome BR have received fishes of Nearctic origin via exchanges with the Río Lerma of the Sonora-Lerma BR within the Trans-Mexican Volcanic Belt (Miller et al. 2005, Domínguez-Domínguez et al. 2011, Beltrán-López et al. 2021).

Unique Patterns: A Comparison with Turtles

Similar methods have been used to determine BRs for aquatic turtles across NoMA, and the major boundaries identified in this study for fishes are not evident among the boundaries observed for aquatic turtles (Ennen et al. 2017). This suggests ecological and historical differences in how aquatic turtles and freshwater fishes colonized the region. Possible significant differences include the fact that even aquatic turtles are capable of overland dispersal, whereas fishes largely can not. On the other hand, turtles tend to be more confined to low elevations, whereas fishes can be widespread at high elevations and (as already noted for the Sierra Madre Occidental) may occur on both sides of a drainage divide. These subtle differences may have influenced the two groups to (at least in some cases) use different dispersal routes among the river drainages of NoMA. Turtles are also present in lower species diversity, in which case smaller differences among assemblages result in quantitative differences (Ennen et al. 2017). Nevertheless, as for fishes, the NoMA region is an area of high turtle beta diversity due to a similar potential for rugged landscapes and high aridity to isolate faunas (Ennen et al. 2020).

Conclusion

We demonstrate that Northern Middle America (NoMA) is composed of seven distinct and expansive biogeographic regions (BR), delimited by three major biogeographic barriers: 1) the Sea of Cortés-Sierra de Juarez-Cerro Gordo, 2) the Río Grande rift-the Sierra Madre Occidental-Mesa Central, and 3) the Trans-Mexican Volcanic Belt-Sierra Madre del Sur-Sierra Madre de Chiapas (Fig. 3). These strong and persistent barriers produced high rates of endemism, often with ancient origin (Spencer et al. 2008, Hoagstrom et al. 2020). Among the northern BRs, high regional aridity further increased faunal isolation. High faunal turnover (beta diversity) among adjacent bioregions implies that the BRs of NoMA harbor some of the most distinctive fish faunas of North and Central America. Further, all but the most remote (i.e. northwestern) BRs of NoMA include a mix of Nearctic and Neotropical fishes, forming unique transitional faunas.

Acknowledgements

Author Contributions

All authors designed the study. CNR and WAM gathered and prepared the data. All authors performed the analyses and wrote and reviewed the manuscript.

Data Availability Statement

All data used in this study is available in the supplemental materials section of this article.

Supplemental Materials

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Table S1. Matrix with presence/absence data for 97 level-6 HydroBASINs and 499 species of obligated freshwater fishes from northern Midddle America and southern United States.

Table S2. Table showing the geographic centroids (latitude and longitude) of each level-6 HydroBASIN included in analysis.

Table S3. Presence absence matrix with seven bioregions and 499 species of obligated freshwater fishes of northern Middle America.

Table S4. Result of the Indicator Species Analysis for each bioregion.

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