

Derivation of the freshwater fish fauna of Central America revisited: Myers's hypothesis in the twenty-first century

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Abstract

Although attempts to understand Central American freshwater fish provincialism date to the 1960s, early efforts lacked the wealth of distributional data now available. Biogeographic work on Central American freshwater fishes has been largely descriptive and regional, and lacked a broader synthesis. Here we use parsimony analysis of endemism (PAE) to elucidate faunistic relationships between major drainages and to delineate areas of endemism. We then perform a Brooks parsimony analysis (BPA) on the resulting areas. The PAE recovered a primary division between four Pacific and six Atlantic slope areas of endemism. In contrast, the BPA recovered two Central American geographic clades, one sharing a history with North America and the other with South America. Fish diversity is uneven across Central America, with greater diversity in areas adjacent to the more species-rich regions of North and South America. In northern and nuclear Central America, the paucity of ostariophysan freshwater fishes such as catfishes and characins (groups that dominate adjacent regions) contrasts with high species richness of poeciliids and cichlids. Results of this study are consistent with Myer's hypothesis that poeciliids and cichlids dispersed to Northern or Nuclear Middle America early in the Cenozoic, long before the Plio-Pleistocene rise of the Isthmus of Panama.

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Introduction

In 1966 George Myers published a landmark study on the origins of freshwater fishes in Central America. Myers observed that the two most diverse groups, poeciliids and cichlids, constitute more than half of all the species in the region, and are “secondary” freshwater fishes of putative South American origin that possess some physiological tolerance to saltwater (*sensu* Myers, 1949; but see Sparks and Smith, 2005). Myers hypothesized that these two groups dispersed to, and diversified in, Central America during the early Cenozoic, long before the Plio-

Pleistocene rise of the Isthmus of Panama. Myers further hypothesized that “primary” freshwater fishes (assumed to have little or no tolerance to saltwater), like characins and catfishes, dispersed into the region much later during the Plio-Pleistocene emergence of the Panamanian landbridge. Myers' (1966) hypothesis served as a cornerstone for explaining the unusual taxonomic composition of Central American freshwater fishes despite being based solely on distributional patterns rather than phylogenetic analyses. The Central American ichthyofauna is unique in the Americas in being dominated by non-ostariophysan species (Miller, 1966; Bussing, 1976, 1985; Rosen, 1976; Smith and Bermingham, 2005; Chakrabarty and Albert, 2011), whereas ostariophysans [catfishes, characins (tetras), electric knifefishes, carps and minnows]

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comprise more than 70% of known freshwater fish species globally (Nelson, 2006; Eschmeyer and Fong, 2013).

Myers's (1966) hypothesis was remarkably prescient given the paucity of biological and geological information available at the time. Modern phylogenetic systematics was still then in its infancy and understanding species interrelationships was coarse by modern standards. In the subsequent 50 years, our knowledge of Central American biodiversity and geological history has increased, and robust hypotheses of the systematic relationships are now available for many groups of freshwater fishes of the region. Our understanding of the geographical distributions of species across Central America has similarly improved. Extensive ichthyological investigations over the past few decades have generated an exponential increase in museum holdings from the region, especially in the Honduran and Nicaraguan Mosquitia (Caribbean coastal plains) that were largely inaccessible in the 1960s (Miller, 1966). These results were published mainly in the form of new species descriptions and regional species inventories (e.g. Belize—Greenfield and Thomerson, 1997; Costa Rica—Bussing, 2002; Nicaragua—Villa, 2002; Panama and Costa Rica—Smith and Bermingham, 2005; Guatemala—Kihn-Pineda et al., 2006; Honduras—Matamoros et al., 2009; El Salvador—McMahan et al., 2013).

Middle and Central American region boundaries

The region that comprises the land mass between the USA and South America, and sometimes including the Caribbean islands and the West Indies, is referred to as Middle America (Winker, 2011). In this paper we recognize Central America as a politically defined subregion of Middle America that includes the seven Central American Countries (i.e. Panama, Costa Rica, Nicaragua, Honduras, El Salvador, Belize, Guatemala) from the Panama–Colombia border west to the Mexican–Guatemalan border and Mexican–Belize border.

Here we present the first synthetic regional analysis of newly acquired taxonomic and distributional datasets to generate a high-resolution biogeographic analysis of Central American freshwater fishes. Our results update and validate the main conclusions of Myers (1966) with the wealth of empirical data now available. The specific aims of this paper are: (i) to use comprehensive distributional data for freshwater fishes in the region to delineate areas of endemism (AOE) as functional biogeographic units, and (ii) to reconstruct the history of biotic connections among these AOE based on available phylogenetic information of the freshwater fish taxa.

Material and methods

Distributional data

Presence/absence data were recorded for 525 freshwater fish species representing 146 genera and 37 families, distributed among 32 drainage basins in Central America, northern Colombia (Río Atrato and Río Magdalena basins) and Southern Mexico (Río Usumacinta drainage, southern Chiapas, Yucatan, Quintana Roo and Campeche (Presence/Absence dataset available from the authors). The freshwater fishes of Central America include 299 valid primary and secondary species in 98 genera and 31 families; Table S1), excluding species from southern Mexico and northern Colombia. Because several taxa range beyond these limits, and to facilitate testing of biogeographic hypotheses, we also included distribution records from adjacent Río Magdalena and Río Atrato basins of northern Colombia (Maldonado-Ocampo et al., 2006, 2008; Mojica et al., 2006) and rivers of southern Chiapas and Mexican portions of the Río Grijalva–Usumacinta drainage (Schmitter-Soto, 1999; Miller et al., 2005). Distributional data were compiled through literature searches of books and peer-reviewed checklists for Panama (Loftin, 1965; Smith and Bermingham, 2005), Costa Rica (Bussing, 2002; Smith and Bermingham, 2005), Nicaragua (Villa, 1982; Smith and Bermingham, 2005; Matamoros et al., 2012a), Honduras (Matamoros et al., 2009, 2012a), El Salvador (McMahan et al., 2013), Guatemala (Kihn-Pineda et al., 2006) and Belize (Greenfield and Thomerson, 1997).

Phylogenetic data

Ten published and two newly generated phylogenies were used for historical biogeographic analysis (Table 1), including examples from all major groups (i.e. families, genera) of freshwater fishes in Central America. These phylogenies include: four Cyprinodontiformes (Rivulidae—Murphy et al., 1999; *Profundulus*—Matamoros et al., 2012b; Fundulidae—Ghedotti and Davis, 2013; Poeciliinae—this study); two Characiformes (*Ctenolucius*—Vari, 1995; *Roeboides*—Lucena, 2000); one Gymnotiformes (*Gymnotus*—Brochu, 2011); one Lepisosteiformes (Wright et al., 2012); three Siluriformes (Callichthyidae—Shimabukuro-Dias et al., 2004; *Rhamdia*—Perdices et al., 2002; Pimelodidae—Hardman and Lundberg, 2006); and one Perciformes (Cichlinae—this study).

Phylogeny reconstruction of Cichlinae and Poeciliinae

Molecular methods. All sequences used in construction of these phylogenetic hypotheses were

Table 1
Phylogenies included in the Brooks parsimony analysis

Taxa	Study
Cyprinodontiformes	
Rivulidae	Murphy et al. (1999)
Profundulidae	Matamoros et al. (2012b)
Poeciliidae: Poeciliinae	This study
Fundulidae	Ghedotti and Davis (2013)
Characiformes	
<i>Ctenolucius</i>	Vari (1995)
<i>Roeboides</i>	Lucena (2000)
Gymnotiformes	
<i>Gymnotus</i>	Brochu (2011)
Lepisosteidae	Wright et al. (2012)
Siluriformes	
Callichthyidae	Shimabukuro-Dias et al. (2004)
<i>Rhamdia</i>	Perdices et al. (2002)
Pimelodidae	Hardman and Lundberg (2006)
Perciformes	
Cichlidae: Cichlinae	This study

taken from GenBank (NCBI—National Center for Biotechnology Information). The cichlid dataset used two nuclear (*Rag1*, *S7*) and three mitochondrial markers (16S, *cyt b* and *COI*). The poeciliinae dataset included one nuclear (*Rag 1*) and two mitochondrial (*cyt b* and *ND2*) markers. Sequences for these datasets were largely derived from Martin and Bermingham (1998), Farias et al. (2001), Concheiro-Pérez et al. (2007), Říčan et al. (2008), Smith et al. (2008) and López-Fernández et al. (2010) for the cichlids, and Schartl (1994), Lydeard et al. (1995) and Hrbek et al. (2007) for the poeciliins. Sequences for each marker were aligned using MAFFT Version 5.3 (Katoh et al., 2005), with final inspection by eye to check for ambiguities. Genes per dataset were concatenated retaining each individual partition for subsequent analyses.

Phylogenetic analyses. Datasets were partitioned by gene and by codon and appropriate models of molecular evolution were selected using JModelTest (Posada, 2008) under the Akaike's Information Criterion (AIC). Bayesian inference analyses were executed in MrBayes (Huelsenbeck and Ronquist, 2001) with four independent runs per dataset of 10 000 000 generations each. Stationarity was assessed with Tracer Version 1.4 (Rambaut and Drummond, 2007) and by assessment of generation versus log-likelihood plots. Trees prior to stationarity were removed as burn-in. A 50% majority rule tree was produced from the post-burn-in trees for each dataset and these are reported in Figure S1. These trees were used for BPA analyses in this study. GenBank accession numbers for all used DNA sequences are presented in Table S2.

Parsimony analysis of endemism

We used PAE (Rosen, 1988) to infer faunistic relationships among Central American river drainages. Parsimony analysis of endemism is a biogeographic technique similar to parsimony-based methods used in phylogenetic reconstruction, in which areas are coded and analysed as operational taxonomic units (OTUs) to determine area relationships based on the shared presence of species. The result of PAE is a branching (tree-shaped) diagram depicting relationships between the species composition of areas (Rosen, 1988; Cra-craft, 1991, 1994). Although there is ongoing debate about the details and interpretation of PAE (Nihei, 2006), results from this analysis have proven to be a useful and important tool for identifying AOE (Morrone and Escalante, 2002; Huang et al., 2008). Nihei (2006) suggested that PAE results may mislead interpretation when using geopolitical boundaries as analysis units instead of geological units as originally proposed. Our use of river drainages is thus a logical and robust geological unit. Crother and Murray (2013) discuss the nested nature of AOE from resulting PAE cladograms, directing attention to the potential of additional complexity in numbers of discoverable AOE.

In order to delimit AOE, we followed the method proposed by Morrone (1994) that consists of the following steps: (i) define operational geographical units (OGU; e.g. river drainages); (ii) construct a presence/absence data matrix; (iii) perform a parsimony analysis of the data matrix; (iv) delimit the OGU or groups of OGUs defined by at least two endemic species; and (v) delineate the boundaries of each AOE. We found that in some previous analyses of endemism, some drainages recovered as nested within or immediately next to defined areas or “provinces” (Smith and Bermingham, 2005; Matamoros et al., 2012a), had no described endemic species. In such cases the newly included drainages were subsumed within a previously defined AOE. For example, the area “Santa María” (Smith and Bermingham, 2005) was defined on the basis of an undescribed species and was therefore subsumed under the AOE “Chiriquí”. All species distributed north of the Río Usumacinta were coded as “Nearctic”, and distributions south of the Río Atrato and Río Magdalena (e.g. Orinoco, Amazon) coded as “South America”. Drainages in Nuclear Middle America and Costa Rica–Panama were coded based on the provinces established in Smith and Bermingham (2005) and Matamoros et al. (2012a), respectively (again, unless they were found to lack a described endemic species).

The distributional dataset consists of a matrix with absence/presence of a species coded 0 and 1,

respectively. Maximum parsimony (MP) analyses were performed using PAUP* (Swofford, 2002) with a data matrix that included a total of 537 species distributed in a total of 32 areas (drainages), with 26 in Central America, four in southern Mexico, and two in northern Colombia. A hypothetical outgroup area with all species coded as absent was included in the matrix to root the ingroup network (Rosen, 1988). Maximum parsimony analyses were performed with heuristic searches using starting trees obtained by means of 100 random sequence additions and then submitted to a tree-bisection-reconnection (TBR) branch-swapping algorithm. Bremer support was calculated as a measure of branch support. Bootstrap frequency for each clade was calculated with 1000 pseudoreplicates (Felsenstein, 2004).

Brooks parsimony analysis

Historical relationships of Central American AOE were elucidated using BPA (Brooks, 1990; Brooks and McLennan, 1991; Brooks et al., 2001) based on phylogenetic data. The use of a historical approach to study Central America freshwater fish AOE is novel. In the past, hypotheses of area relationships for the region have been developed through approaches that do not rely on phylogenetic data, such as clustering analysis (Smith and Bermingham, 2005; Matamoros et al., 2012a). Our BPA uses phylogenetic data to infer historical relationships between AOE (Brooks et al., 2001). Brooks parsimony analysis uses the geographic distributions of both species and higher taxa as evolutionary markers to infer area relationships (Van Veller et al., 2002; Sigrist and Carvalho De, 2009). Brooks parsimony analysis was implemented with the following steps. First, all phylogenies (Table 1) were turned into area cladograms by replacing OTUs with the AOE in which they occur. Second, all internal clades and terminals were number coded for representation in the data matrix. Third, a data matrix was constructed with AOE as OTUs and the number-coded clades as characters, with each internal and external clade coded in the data matrix as absent or present for all AOE. Additional areas were also necessary for some distributions (Nearctic, South America and Greater Antilles). Fourth, all individual data matrices were concatenated into a single super data matrix. Fifth, the area cladogram was rooted with a hypothetical outgroup area coded by the absence of any taxa (Crisci et al., 2003). Sixth, MP analyses were performed in PAUP* (Swofford, 2002), using heuristic searches with TBR for 100 random additions. Bootstrap frequency for each clade was calculated with 1000 pseudoreplicates (Felsenstein, 2004).

Results

Alpha diversity

As observed by Myers (1966) and Miller (1966), species richness in the freshwater fishes of Central America is substantially higher in areas located adjacent to the more species-rich regions of North and South America. The species density of Central American freshwater fishes as a whole is comparable to the ca. 500 described species found in Mexico, which covers an area of 1 964 380 km² (Miller et al., 2005). Lower Central America (Darién and adjacent region of Panama) harbours 156 species (52.1% Central American fishes), followed by the Río Usumacinta drainage in northern Central America with 94 species (31.4%; Table S1). In general, fish assemblages in lower Central American (Chagres, Tuira, Bocas and Chiriquí-Santa Maria) are dominated by Characidae (tetras), whereas in northern and nuclear Central America (from southern Nicaragua to Grijalva-Usumacinta) Poeciliidae (guppies, swordtails) and Cichlidae (cichlids in the tribe Heroini) are the most speciose (Table S1), contributing 68 and 56 species (38.2%, 31.2%) respectively, while Characidae makes up a relatively small portion (10.1%) of the biodiversity of freshwater fishes in this area.

Parsimony analysis of endemicity of Central American freshwater fishes

The PAE of Central American freshwater fish species distributions yielded a single most parsimonious tree topology, with 781 steps and a consistency index (CI) of 0.69 (Fig. 1). This topology has a basal separation between Pacific and Atlantic slope drainages, demonstrating the importance of recognizing distinct freshwater fish assemblages along each slope of Central America. The Chagres on the Caribbean slope of lower Central America is the only exception, being nested within the Pacific slope systems (Fig. 1).

A list of endemic species diagnosing all AOE is presented in Table 2. Four AOE were recovered in the Pacific slope rivers of Central America (Fig. 1). The first includes the Pacific-draining rivers of northern Central America, specifically the Honduras–El Salvador–Guatemala province of Matamoros et al. (2012a). Four additional drainage systems were recovered alongside this area (Fig. 1), including two in Guatemala (Río Samala, and Río Suchiate near the Mexico border), as well as one in Mexico (small rivers in southern Chiapas). No endemic species are known in these three drainages, and they were therefore combined with the Honduras–El Salvador–Guatemala (of Matamoros et al., 2012a) and referred to here as Chiapas–Nacaome. This AOE encompasses all Pacific riv-

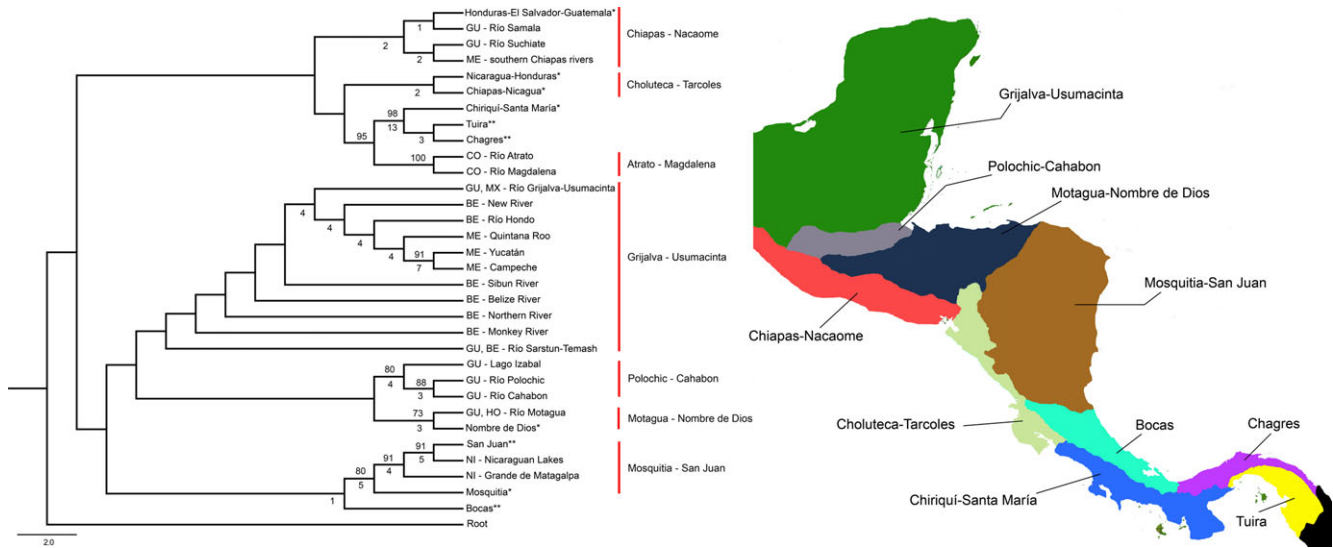


Fig. 1. Results of parsimony analysis of endemicity depicting similarity in the species-composition of areas of endemism (AOE) in Central America and southern Mexico. Area of endemism names are shown at right of terminals on the tree. Terminals without additional names retain original names for the AOE. Bootstrap values > 50% are above the nodes and Bremer support values are below. Map showing location and boundaries of the AOE to the right.

ers in Guatemala to the Río Choluteca (Honduras) in Honduras, all rivers in El Salvador that are part of the Río Lempa drainage (McMahan et al., 2013) and rivers from the Pacific slope of southern Chiapas (Mexico).

Two AOE were recovered in previous studies—Nicaragua–Honduras (*sensu* Matamoros et al., 2012a) and Chiapas–Nicaragua (*sensu* Smith and Bermingham, 2005). Each of these areas harbours only one endemic species, so they were joined together and formed the Choluteca–Tarcoles AOE. The Nicaragua–Honduras area (*sensu* Matamoros et al., 2012a) includes the Río Choluteca in Honduras and all rivers through the Pacific of Nicaragua. The Chiapas–Nicaragua area (*sensu* Smith and Bermingham, 2005) includes drainages of the Nicoya Peninsula to the Río Tarcoles in Costa Rica.

Four AOE cluster together from lower Central America, the Río Magdalena and the Río Atrato in northern South America. Three of these are provinces from Smith and Bermingham (2005) and are here recognized as the Chagres, Tuira and Chiriquí–Santa María AOE (Fig. 1). The Chiriquí–Santa María AOE spans rivers from the Río Pirrís in Costa Rica to the Río Sajalices in Panama. As previously mentioned, because Smith and Bermingham (2005) recognized these provinces based on one undescribed species, they have been combined here. The Chagres and Tuira AOE encompass the Río Chagres and Río Tuira basins, respectively, in Panama. The Río Chagres is an Atlantic drainage; however, its recovery with Pacific systems is not surprising given the number of taxa

shared with neighbouring systems. Finally, the Río Atrato and Río Magdalena in northern Colombia each harbour endemic species; although grouped together in this study we do not suggest they represent a single AOE, as they lie outside our focal region of Central America.

The Atlantic slope of Central America consists of three main regions and six AOE, including the Chagres AOE discussed above. The Grijalva–Usumacinta AOE includes the Río Grijalva–Usumacinta, as well as all rivers of the Yucatan Peninsula and Belize. Unlike the Río Atrato and Río Magdalena, this is considered a single AOE given that portions of this system flow through Central America. Three drainages in Guatemala (Lago Izabal, Río Polochic and Río Cahabon) harbour shared endemic species and are recognized here as the Polochic–Cahabon AOE, spanning the Río Polochic, Río Cahabon and Lago Izabal/Río Dulce in Guatemala.

The Río Motagua and the rivers of Nombre de Dios (*sensu* Matamoros et al., 2012a) were recovered as sister. Both areas harbour one endemic species exclusive of the other, and together are recognized here as a single AOE, Motagua–Nombre de Dios. The Motagua–Nombre de Dios AOE includes the Guatemalan and Honduran portions of the Río Motagua drainage and rivers in the Nombre de Dios region of Honduras, from the Río Chamelecon to the Río Lis Lis. The Río San Juan drainage, the Nicaraguan Lakes, the Río Grande de Matagalpa, and the river drainages throughout the Honduran and Nicaraguan region of La Mosquitia form a fifth AOE in the Atlantic slope

Table 2

List of endemic species diagnosing recovered areas of endemism from the parsimony analysis of endemism. Areas of endemism are arranged in order from north to south within Pacific and Atlantic slopes

Area of endemism	Species
Pacific	
Chiapas–Nacaome	Heptapteridae: <i>Rhamdia parryi</i> , Profundulidae: <i>Profundulus guatemalensis</i> , Poeciliidae: <i>Brachyrhaphis hartwegi</i> , <i>Poecilia marcellinoi</i> , <i>Poecilia salvatoris</i> , <i>Poeciliopsis fasciata</i> , Cichlidae: <i>Amatitlania coatepeque</i> , <i>Amphilophus macracanthus</i> , <i>Paraneetroplus guttulatus</i>
Cholulteca–Tarcoles Chiriquí–Santa María	Poeciliidae: <i>Poeciliopsis santaelena</i> , Cichlidae: <i>Amphilophus hogaboomorum</i>
Tuira	Characidae: <i>Hyphessobrycon savagei</i> , <i>Pseudocheirodon terrabae</i> , <i>Pterobrycon myrnae</i> , <i>Roeboides ilsea</i> , Lebiasinidae: <i>Piabucina boruca</i> , Heptapteridae: <i>Imparfinis lineatus</i> , Rivulidae: <i>Cynodonichthys glaucus</i> , <i>Cynodonichthys uroflammeus</i> , Poeciliidae: <i>Poeciliopsis paucimaculata</i> , Cichlidae: <i>Amphilophus altifrons</i> , <i>Amphilophus diquis</i> , <i>Amphilophus lyonsi</i> , <i>Cryptoheros sajica</i>
	Characidae: <i>Bryconamericus bayano</i> , Crenuchidae: <i>Characidium marshi</i> , Loricariidae: <i>Rineloricaria altipinnis</i> , <i>Sturisomatichthys citurensis</i> , Poeciliidae: <i>Neoheterandria cana</i> , Cichlidae: <i>Amphilophus calobrensis</i> , “ <i>Cichlasoma</i> ” <i>tuyrense</i>
Atlantic	
Grijalva–Usumacinta	Characidae: <i>Astyanax altior</i> , <i>Brammocharax baileyi</i> , <i>Brammocharax dorioni</i> , Rivulidae: <i>Millerichthys robustus</i> , Profundulidae: <i>Profundulus candalarius</i> , <i>Profundulus hildebrandi</i> , Fundulidae: <i>Fundulus grandissimus</i> , <i>Fundulus persimilis</i> , Poeciliidae: <i>Carlhubbisia kidderi</i> , <i>Gambusia sexradiata</i> , <i>Gambusia yucatanana</i> , <i>Pseudoxiphophorus attenuatus</i> , <i>Pseudoxiphophorus cataractae</i> , <i>Pseudoxiphophorus diremptus</i> , <i>Pseudoxiphophorus obliquus</i> , <i>Gambusia echeagarayi</i> , <i>Heterophallus milleri</i> , <i>Phallichthys fairweatheri</i> , <i>Poecilia petenensis</i> , <i>Poecilia sulphuraria</i> , <i>Poecilia teresae</i> , <i>Poecilia velifera</i> , <i>Poeciliopsis hnlickkai</i> , <i>Scolichthys greenwayi</i> , <i>Scolichthys iota</i> , <i>Xenodexia ctenolepis</i> , <i>Xiphophorus alvarezi</i> , <i>Xiphophorus signum</i> , Cyprinodontidae: <i>Cyprinodon artifrons</i> , <i>Cyprinodon beltrani</i> , <i>Cyprinodon labiosus</i> , <i>Cyprinodon maya</i> , <i>Cyprinodon simus</i> , <i>Cyprinodon verecundus</i> , <i>Floridichthys polyommus</i> , <i>Garmanella pulchra</i> , Cichlidae: <i>Theraps nourissati</i> , “ <i>Cichlasoma</i> ” <i>grammodes</i> , <i>Theraps pearsei</i> , <i>Cryptoheros chetumalensis</i> , <i>Paraneetroplus argenteus</i> , <i>Paraneetroplus bifasciatus</i> , <i>Paraneetroplus breidohri</i> , <i>Paraneetroplus hartwegi</i> , <i>Paraneetroplus melanurus</i> , <i>Petenia splendida</i> , <i>Rocio gemmata</i> , <i>Rocio ocotol</i> , <i>Theraps intermedius</i> , <i>Theraps gibbiceps</i> , <i>Theraps heterospilus</i> , <i>Theraps lentiginosus</i> , <i>Thorichthys affinis</i> , <i>Thorichthys helleri</i> , <i>Thorichthys meeki</i> , <i>Thorichthys passionis</i> , <i>Thorichthys socolofi</i>
Polochic–Cahabon	Poeciliidae: <i>Carlhubbisia stuarti</i> , <i>Pseudoxiphophorus litoperas</i> , <i>Poecilia rositae</i> , Cichlidae: <i>Archocentrus spinosissimus</i> , <i>Cryptoheros spilurus</i>
Motagua–Nombre de Dios Mosquitia–San Juan	Characidae: <i>Hyphessobrycon milleri</i> , Cichlidae: <i>Theraps microphthalmus</i> , <i>Theraps wesseli</i>
	Characidae: <i>Astyanax nasutus</i> , <i>Brammocharax bransfordii</i> , Rivulidae: <i>Cynodonichthys fuscolineatus</i> , Poeciliidae: <i>Brachyrhaphis holdridgei</i> , <i>Phallichthys tico</i> , <i>Xenophallus umbratilis</i> , Cichlidae: <i>Amphilophus amarillo</i> , <i>Amphilophus astorqui</i> , <i>Amphilophus chanco</i> , <i>Amphilophus flaveolus</i> , <i>Amphilophus globosus</i> , <i>Amphilophus sagittae</i> , <i>Amphilophus superciliosus</i> , <i>Amphilophus xiolaensis</i> , <i>Amphilophus zaliosus</i> , <i>Hypsophrhys nematopus</i> , <i>Hypsophrhys nicaraguensis</i>
Bocas	Rivulidae: <i>Cynodonichthys birkhahni</i> , <i>Cynodonichthys kuelpmanni</i> , <i>Cynodonichthys rubripunctatus</i> , <i>Cynodonichthys wassmanni</i> , Poeciliidae: <i>Priapichthys puetzi</i> , Cichlidae: <i>Amphilophus bussingi</i> , <i>Cryptoheros myrnae</i>
Chagres	Characidae: <i>Odontostilbe mitoptera</i> , <i>Roeboides carti</i> , Rivulidae: <i>Cynodonichthys montium</i>

of Central America. While there are endemic species in the Río San Juan and Nicaraguan Lakes, no species are endemic to Río Grande de Matagalpa or rivers in La Mosquitia; therefore, all four of these areas are included as a single AOE and referred to as Mosquitia–San Juan following Matamoros et al. (2012a). The Bocas AOE (*sensu* Smith and Bermingham, 2005) covers an area from the Río Sarapiquí in Costa Rica to the western border of the Río Chagres basin in Panama.

Overall, endemism in Central America is greater in northern regions (Table 2). In the Grijalva–Usumacinta AOE, 58 species out of a total of 94 (59.2%; Table 2) are endemic. This level of endemism is in stark contrast to the 3.1% and 6.7% endemism recovered in the Chagres and Tuira AOE, respectively, in lower Central America. The AOE from nuclear Middle America show low levels of endemism, which is consistent with past

work (Matamoros et al., 2012a); however, the Mosquitia–San Juan AOE has 18.1% endemism, a result largely in part of endemic cichlids (*Amphilophus* spp.) in the Nicaraguan Lakes. On the Pacific slope, the Nicoya–Tarcoles (16 species) and Cholulteca–Nicaragua (35 species) AOE are among the most species-poor in all of Central America, although the Chiapas–Nacaome AOE has 34.3% endemism. Species endemic to these areas belong primarily to the families Poeciliidae (five species) and Cichlidae (five species), and not ostariophysan primary freshwater fishes, corroborating results of Matamoros et al. (2012a).

Brooks parsimony analysis

The two main branches of the general area cladogram (Fig. 2) are geographically disjunct. A more northern branch includes AOE in the Nearctic realm

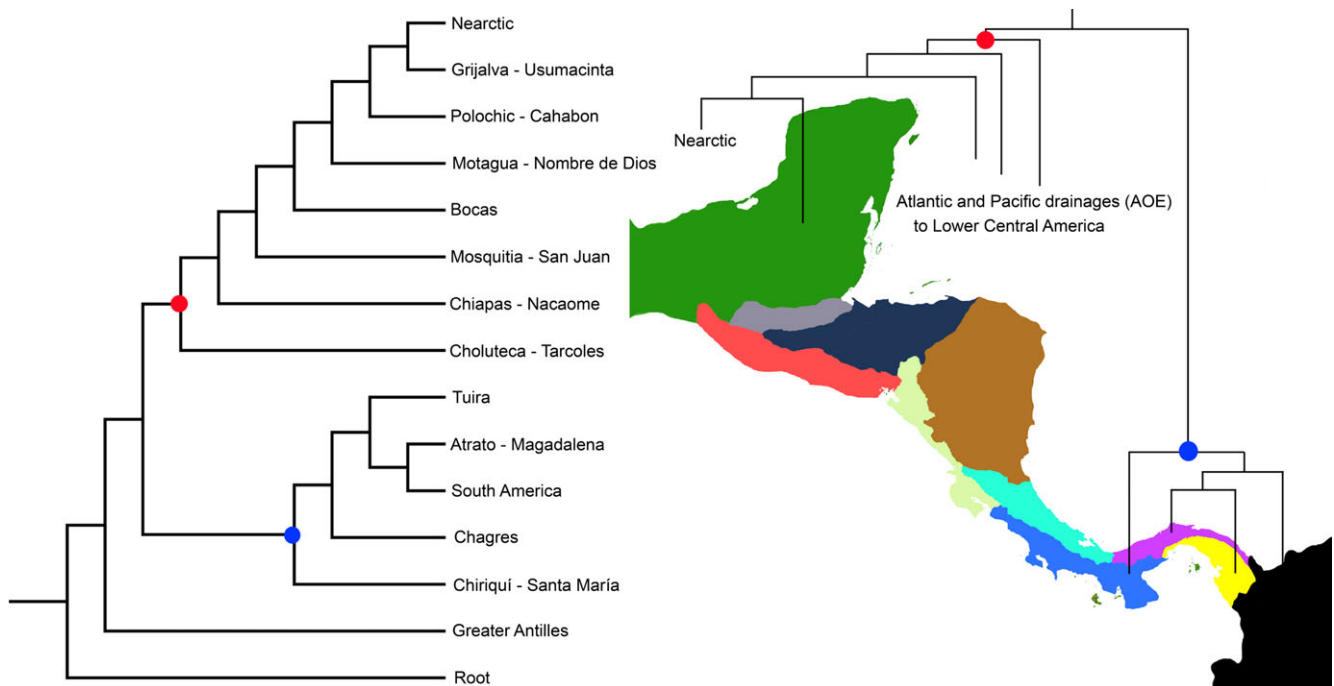


Fig. 2. Results of Brooks parsimony analysis depicting a general area cladogram for 10 clades of Central American freshwater fishes. Terminals are areas of endemism. Map to the right shows area cladogram overlaid on map of region with the AOE delineated.

and from the Grijalva–Usumacinta and Chiapas–Nacaome to Bocas and Choluteca–Tarcoles. This latter group of AOE includes rivers from both Atlantic and Pacific slopes, indicating that from a deeper-time historical perspective, there has been substantial shared history between river basins of these two slopes. The second branch includes AOE from lower Central America (Chiriquí–Santa María, Chagres and Tuira). These three AOE were recovered in a close relationship between Atrato–Magdalena in northern Colombia, as well as South American rivers (e.g. Orinoco and Amazon). These results indicate that AOE in lower Central America share a history with northern Colombia (Río Atrato and Río Magdalena) and South America.

Discussion

Tobler’s First Law of Geography states “everything is related to everything else, but near things are more related than distant things” (Tobler, 1970). This principle applies to both the species content and phylogenetic structure of Central American freshwater basins, as assessed by PAE and BPA respectively, both of which show the strong influence of geographic proximity (Figs 1 and 2). However, the results of these two analyses differ strongly, and these differences describe the different but overlapping scales of evolutionary change addressed by the two methods.

Contemporary biogeographic patterns

The results of the PAE recovered well-defined Pacific and Atlantic assemblages of freshwater fishes along the coasts of Central America (Fig. 1). This basal separation of drainages by slope in the analysis of modern species distributions highlights the role of the interior highlands of Central America as a barrier to dispersal in freshwater fishes. This result also highlights the potential importance of dispersal along coastal plains as among the most important determinant of species content in local assemblages. The entirety of Pacific AOE cluster together, from the Chiapas in southern Mexico to the Tuira in eastern Panama, and all Atlantic AOE but one cluster together, from the Grijalva–Usumacinta in southern Mexico to the Bocas in eastern Costa Rica and western Panama. The single exception is the position of the Chagres AOE on the Atlantic slope of Panama, which clusters with Pacific slope AOE of Panama.

Fish-species richness is greater in northern than lower Central America. At this scale these results are largely congruent with the results of Miller (1966) and Bussing (1976). However, previous studies failed to detect finer-scale biogeographic structure in Central America, probably due to insufficient information on species distributions. More recent studies show greater biogeographic structure in Central America (Smith and Bermingham, 2005; Matamoros et al., 2012a), but these studies were limited to only smaller regional

portions of Central America. Smith and Bermingham (2005) described seven biogeographic provinces in Lower Central America, whereas Bussing (1976) proposed only two provinces for the same area. More recently, Matamoros et al. (2012a), in a biogeographic study that included river drainages from nuclear Middle America, found four provinces where Bussing (1976) reported two. Furthermore, in earlier analyses such as Miller (1966), the areas of eastern Honduras and northwestern Nicaragua (the Honduran and Nicaraguan Mosquitia) were not assigned provinces because of the paucity of distributional data for that region at the time. Our results indicate that the Nicaraguan and Honduran Mosquitia form a large continuous AOE that comprise most of the nuclear Middle America Caribbean lowlands.

Individual species of freshwater fishes have been relatively more successful invading Central America from the south than from the north. For instance, one species of *Gymnotus* (*G. maculosus* Albert and Miller, 1995) and three species of *Rhamdia* extend as far north as southern Mexico (Miller et al., 2005), and one species of cichlid (*Herichthys cyanoguttatus* Baird & Girard, 1854) and a characid [*Astyanax mexicanus* (De Filippi, 1853)] naturally occur in the southern USA. However, only three species of North American freshwater fishes have successfully invaded Central American freshwaters; the blue-catfish [*Ictalurus furcatus* (Valenciennes, 1840)] and the Usumacinta buffalo [*Ictiobus meridionalis* (Günther, 1868)] reach as far as northern Guatemala, and the tropical gar (*Atractosteus tropicus* Gill, 1863) has successfully dispersed into lower Central America (Miller, 1966; Myers, 1966; Bussing, 2002; Miller et al., 2005).

Some species from northern Middle American have dispersed to, and contribute to, assemblages in lower Central America. *Gambusia nicaraguensis* Günther, 1866 is widely distributed from northern Middle America through Panama and one species of *Gambusia* (*G. lemaitrei* Fowler, 1950) is found in Colombia and Venezuela. One species of *Poeciliopsis* is found from Central America through northern Colombia [*P. turrubarensis* (Meek, 1912)] and several *Poeciliopsis* species may have evolved in lower Central America [e.g. *P. elongata* (Günther, 1866), *P. retropinna* (Regan, 1908) and *P. paucimaculata* Bussing, 1967]. Finally, one species of cichlid [*Paraneotroplus maculicauda* (Regan, 1905)] has dispersed from northern Middle America throughout the Atlantic drainages of Central America to Panama.

Historical biogeographic patterns

In contrast to the results of analysis of species distributions, the most important determinant of deeper phylogenetic structure among Central American fresh-

water fishes is proximity to neighbouring regions of North and South America (Albert et al., 2011). Here the results are dominated by the contemporary and historical sharing of taxa in lower Central America with adjacent areas of South America, and not with other portions of Central America. The distribution of freshwater fishes in lower Central America (particularly the Darién region of eastern Panama) indicates a closer shared history with northern South America than the rest of Central America. Similar biogeographic patterns have been reported in Central America for snakes (Daza et al., 2010). Additionally, while examining biogeographic relationships with a combined data set that included plants, insects, amphibians and reptiles across Middle and South America, Echeverry and Morrone (2013) found that Lower Central American (Panama and Costa Rica) regions were included in their South American subregion. Those results are congruent with our findings; however, Nuclear Central America (Nicaragua, Honduras and El Salvador) in Echeverry and Morrone (2013) has a mixed biogeographic signal divided by a strong South American subregion that expands into the Atlantic slope of Nuclear Central America and a Mesoamerican subregion (*sensu* Echeverry and Morrone, 2013; Sánchez-González et al., 2013) that covers the Pacific slope of Nuclear Central America. Our BPA results partially agree with Echeverry and Morrone (2013) in that Lower Central American freshwater fishes show South American affinities, but the entire region of Nuclear Central America in our results is of Northern Middle American origin. The differences in our results when compared with those of Echeverry and Morrone (2013) may be due to the fact that this study is focused only on freshwater fishes versus multiple taxa, and also the fact that freshwater fishes are largely constrained to freshwater connections (Unmack, 2001; Smith and Bermingham, 2005) and do not necessarily reflect the same biogeographic patterns as terrestrial taxa. Our results are congruent with geological information on the timing of movements of the Chocó Block (Marshall, 2007; Pindell and Kennan, 2009). Our results indicate that areas of lower Central America, especially the Tuira, Chagres and Chiriquí–Santa María AOE, should be considered South American, at least for freshwater fishes. The direct implications of this are evident when studying evolutionary and biogeographic patterns of neotropical fishes, and quite likely other neotropical taxa. The use of Central or Middle American political boundaries should be avoided, because these political delineations are biologically empty and do not represent natural biogeographic/biological breaks.

The results of this study suggest a lengthy history of faunal exchanges between the Tuira and Chagres basins of southern Panama and the adjacent Río

Atrato and Río Magdalena basins of northern Colombia. Exchanges between these areas have been so strong that the adjacent assemblages of freshwater fishes in the Chagres and Mosquitia–San Juan areas are quite distinct, with a very low number of shared species. The rise of the Isthmus of Panama appears to have allowed only a small number of reciprocal exchanges between basins in lower Central America (e.g. Tuira, Chagres, Bocas and Chiriqui–Santa Maria) and trans-Andean (i.e. western slope drainages from the Andes mountain range) regions of northern South America (Albert et al., 2006; Chakrabarty and Albert, 2011). South American species that dispersed north into Middle America include some characiforms (e.g., *Cyphocharax* and *Piabucina* spp.), and Middle American species that dispersed south include some cichlids (*Tomocichla* spp.).

Interpreting BPA in freshwater systems

Results of BPA are widely interpreted in the literature as general area cladograms, depicting the shared history of regions inhabited by taxa used in the analysis (Albert and Carvalho, 2011). This interpretation is valid to the extent that the taxa under study diversified under a common set of geographic influences affecting dispersal, extinction and speciation. Under such conditions a general area cladogram may be interpreted as a consensus history of the areas inhabited by the taxa under study. Because BPA incorporates evolutionary information from multiple independent clades, it can sample phylogenetic signals from multiple elements of a whole fauna. This approach has the advantage of reducing the effects of the idiosyncratic histories of individual taxa.

However, it is important to note that in the context of freshwater river basins, a strictly branching general area cladogram does not fully represent the complete history of connections among adjacent drainages. River basins exchange tributaries by erosion across their watersheds, and the history of such stream-capture events always results in a reticulated pattern of connections among basins. This is because each capture event simultaneously separates and connects portions of adjacent basins (i.e. geodispersal; Albert and Crampton, 2010; Albert et al., 2011). In this regard, the evolution of freshwater fish clades is very different from that of river basins in which they live. It is interesting to note the observed value of 0.60 for the consistency index (CI) in the BPA (Fig. 2) is slightly higher than the theoretically expected value of 0.50, the latter of which is predicted when vicariance and geodispersal contribute equally to net diversification across watersheds (Albert et al., 2011). A CI with a value > 0.50 indicates an excess in the contribution of vicariance over geodispersal to the evolutionary pro-

cesses (i.e. speciation and extinction) that produce observed phylogenetic patterns.

River or stream capture is a perennial force affecting the biogeographic history of freshwater organisms (Huber, 1998; Lundberg et al., 1998; Hewitt, 1999; Avise, 2000). Important fluvial mechanisms affecting fish distributions in Central America may have been lateral stream capture and drainage rearrangements that facilitated movements of fishes along the coastal plains (Huber, 1998; Albert et al., 2006). These events included the episodic merging and separation (or drowning) of river mouths associated with Pleistocene sea-level changes (Rull, 1999; Albert et al., 2011). Headwater capture was presumably much less important in Central America, given the relatively few numbers of species that occur at higher elevations, and the relatively few species shared between Pacific and Atlantic slope basins.

As in any biogeographic study, the results reported herein are highly sensitive to the quality and robustness of distributional and phylogenetic information. The datasets assembled for this study are the most exhaustive to date regarding the distributions and interrelationships of Central American freshwater fishes and include a great deal of new phylogenetic and distributional information. Our results show that the biogeographic structure of modern species distributions, as assessed by PAE, was strongly influenced by dispersal along the Pacific and Atlantic coastal plains, and limited by barriers across drainages in the mountainous interior highlands. In contrast, evidence from the phylogenetic relationships of multiple species-rich taxa (BPA) highlight the role of the region's complex tectonic history and rare long-distance dispersal events in the formation of the regional ichthyofauna. As anticipated by Myers (1966), Rosen (1976) and many subsequent authors, one of the most striking patterns is the extreme paucity of primary freshwater fish species, notably ostariophysans, in northern and nuclear Central America. This contrasts with the high species richness of poeciliids and cichlids that originated in South America, became emplaced in northern Middle America in the Paleogene, and later came to dominate the freshwater fish assemblages throughout all of Central America (Morales-Cazan and Albert, 2012).

These results are consistent with a model in which poeciliids and cichlids arrived in northern and/or nuclear Middle America long before the commonly cited Plio-Pleistocene rise of the Isthmus of Panama (Myers, 1966; Rosen, 1976). Recent biogeographic studies in poeciliids (Hrbek et al., 2007) and cichlids (Říčan et al., 2012) concur with the earlier hypotheses of Myers and Rosen, indicating that members of these two families arrived in Northern Middle America by means of an Upper Cretaceous or Paleogene connection between Northern Middle America and

South America, perhaps by the GAARlandia (Greater Antilles and Aves Ridge) land bridge (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2004) or a proto-Greater Antillean landbridge connection (Rosen, 1976; Chakrabarty, 2006; Chakrabarty and Albert, 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Cichlinae and Poeciliinae Bayesian consensus trees (50% majority rule). Numbers above nodes are posterior probabilities.

Table S1. Central American freshwater fishes distribution by areas of endemism.

Table S2. Summary table of GenBank accession numbers for all sequence data used in this study.