Northern South America

Magdalena and Maracaibo Basins

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The Geological History, Topography, and Hydrology of Northern South America

The river basins of Northern South America (NSA) vary widely in the taxonomic composition of their freshwater fishes. Rivers of high species richness and very high endemism are interspersed between arid regions with depauperate faunas (Dahl 1971; Mago-Leccia 1970). These variations are products of existing climatic and hydrological conditions and also reflect the dramatic historic transformations that these drainages have undergone. Plate tectonics and the Andean orogeny set the stage for diversification of aquatic biotas of the region (Eigenmann 1920b, 1920c; Albert et al. 2006).

For most of South America's history as an independent continent the proto-Orinoco-Amazon system emptied into the Caribbean Basin, a western arm of the Tethys Sea. As time went by, the proto-Orinoco-Amazon mega river system became fragmented by tectonic events. In NSA the rise of the various branches of the Andean mountain ranges (the Central and Eastern Cordilleras in Colombia, and the Venezuelan or Mérida branch of the Andes) and the movements of the associated tectonic plates (South American and Caribbean plates and Maracaibo microplate) eventually divided the fishes into separate biotas. These tremendous geological transformations were accompanied by important fluctuations in sea level. Marine incursions such as that of the Early Pliocene, when sea levels reached around 100 meters above current levels (Nores 2004), could easily have exterminated a large portion of the freshwater fishes of Magdalena and Maracaibo, with their low, extensive floodplains. Marine regressions were repeated events with very different effects. Between 20 and 18 thousand years ago (Ka), during the last glacial maximum, sea levels dropped more than 100 meters, and at about 8 Ka they again fell to about 15 m below current levels along the coasts of NSA (Rull 1999). The exposed floodplains propitiated interconnections of fluvial systems and, as a consequence, the potential for dispersal of freshwater fishes along the coasts. Along with

sea-level changes, climatic changes associated with glacial versus interglacial periods, such as the migration of the Intertropical Zone of Convergence, have created today's mosaic of wet and dry drainages along the coasts of NSA (C. González et al. 2008).

Previous biogeographic analyses of freshwater fishes of NSA have had different scopes. Authors like Carl E. Eigenmann and Leonard P. Schultz presented similar scenarios for the origin of trans- and cis-Andean fish faunas of NSA and analyzed its complexity in light of both dispersal and vicariance events. During the second half of the past century, many authors (Fowler 1942; Géry 1969; G. Myers 1966; Mago-Leccia 1970; Dahl 1971; Taphorn and Lilyestrom 1984; Galvis et al. 1997) recognized zoogeographic entities in NSA, qualitatively associating drainage area, species richness, geographic boundaries, and geological history. The general tendency was to continue the qualitative recognition of large-scale biogeographic units (e.g., the Caribbean drainage). Previous analyses of similarity between the Magdalena and Maracaibo basins (Pérez and Taphorn 1993) provided one of the first quantitative studies to compare faunas, ideas on dispersal, and the role of Pleistocene refugia for freshwater fishes. Later analyses have concentrated on biogeographic regionalization and the role of dispersal (Smith and Bermingham 2005; Rodríguez-Olarte et al. 2009), parsimony analysis of endemism (Hubert and Renno 2006), phylogenetic analysis using mitochondrial DNA (Perdices et al. 2002), and the integration of biological records with geologic history to explain historic events (Lovejoy et al. 2006).

In this chapter we provide detailed consideration of small, local, river fish faunas and apply techniques of classification and ordination to them, along with analyses of species richness and distribution patterns of freshwater fishes of the coast of NSA, to delimit biogeographic units and relate them to historical and ecological variables.

BRIEF GEOLOGICAL HISTORY OF NORTHERN SOUTH AMERICA

The diverse drainages of modern NSA are derived from the proto-Orinoco-Amazon river basin. This vast paleodrainage encompassed the eastern slopes of the central mountain range of Colombia (Magdalena), the western drainages of the Guiana

Shield, the foreland basin of the eastern slopes of the Andes, the western edge of the Brazilian Shield, and perhaps even part of what is today the upper Paraná River drainage (Iturralde-Vinent and MacPhee 1999; Hoorn et al. 2006; Díaz de Gamero 1996). From the Eocene to the Miocene the subduction of the Caribbean plate beneath the South American plate produced the Andean uprising of the Central Cordillera of Colombia (Erikson and Pindell 1993). This began the isolation of the region, eventually isolating the Pacific drainages from the rest of NSA. In what is now the Lake Maracaibo Basin, the major south-to-north drainage of South America, the proto-Orinoco-Amazon, emptied into the Caribbean Sea (as it had done since the late Cretaceous).

In the Pliocene, with the closing of the Isthmus of Panama, a definitive geological connection united Lower Mesoamerica with NSA (Iturralde-Vinent and MacPhee 1999). The continued ascent of the northern Andes associated with the Magdalena and Maracaibo regions reoriented the course of the proto-Orinoco-Amazon, and a delta formed in the sedimentary plains of northern Colombia and Venezuela. The Eastern Cordillera of Colombia ended its major ascent in the Early Pliocene (Gregory-Wodzicki 2000), isolating the Magdalena, and the rapid rise of the Andes of Mérida in the Late Pliocene (Mattson 1984) finalized the separation of the Lake Maracaibo Basin from the proto-Orinoco-Amazon river (Díaz de Gamero 1996).

The central coastal mountain range in Venezuela had its origin prior (upper Cretaceous) to that of the Andes of Mérida from which it is separated by the Yaracuy depression (González de Juana et al. 1980). Thus there are two different mountain ranges of different ages (Coastal and Interior) that have an west-east orientation and that flank the elongate tectonic depression which is occupied today by Lake Valencia. The continued rotation of the Maracaibo microplate caused an even greater rise in the Coastal range and the highlands along the eastern coast of NSA, which led to the complete isolation of the region draining toward the Golfo Triste and of the drainages coming from the Turimiquire massif and the mountain system of the Araya and Paria peninsulas, as well as the drainage of the Unare River (Mattson 1984).

MODERN TOPOGRAPHY AND HYDROGEOGRAPHY

Climate in NSA varies dramatically. Areas such as southern Lake Maracaibo and the Atrato drainages have high rainfall, while the nearby Guajira peninsula is extremely arid. The Perijá Mountains, by blocking the moisture-laden trade winds, create a humid funnel effect over Lake Maracaibo and the subsequent predominantly dry climate on the other side of the mountains in the Magdalena drainage. In most drainages, there are two distinct seasons per year, wet and dry, that vary with latitude, altitude, and the configuration of nearby mountains.

At the westernmost corner of South America, on the border of Colombia and Panama, we find the Tacarcuña Mountains, which reach to 1,910 m, and the coastal ridge of Baudó (to 1,810 m). This Pacific versant is divided into three zones: (1) a coastal plain between the mouths of the Mira and San Juan Pacific rivers, furrowed by two rivers, the Patía and the Dagua, (2) a zone that continues to the Isthmus of Panama, in which the Baudó ridge creates a coastal landscape of steep cliffs and small bays, and (3) a valley formed between the Baudó ridge and the Western Cordillera, with the Atrato River to the north, and the San Juan and Baudó to the south. Of all these, the Atrato has the largest freshwater floodplain. This region is one of the wettest in the world, and precipitation

can surpass 10,000 mm/yr, causing high discharge rates for the region's rivers: Atrato (4,500 m^3/s), San Juan (2,721 m^3/s) (J. Mojica et al. 2004).

The Magdalena drainage (length. 1,540 km; maximum peaks. 3,800 m in Páramo Las Papas) forms an extensive intermountain valley between the Eastern and Central Cordilleras. Its principal tributary, the Cauca (1,350 km; 3,000 m, Laguna del Buey), runs parallel to the Magdalena's main channel between the Western and Central Cordilleras. The Cauca from its origin down to about 2,000 m is torrential, but between 1,500 and 900 m the valley widens, slopes lessen, and the river meanders through a more ample floodplain. About 500 km farther downstream it flows through a deep, narrow canyon and passes through a series of rapids that are an insurmountable geographic barrier for many species of fishes. These two rivers conjoin in the lowlands in an extensive floodplain of some 22,000 km^2. The Magdalena River discharges an annual average of 7,300 m^3/s into the Caribbean Sea, with one of the highest sediment loads of the continent (Restrepo et al. 2006).

The Lake Maracaibo drainage (basin, c. 80,000 km^2; lake, 12,870 km^2) is flanked to the west by the Perijá Mountains, to the east by the Mérida branch of the Venezuelan Andes (or Mérida Andes), and to the south by the union of these. Lake Maracaibo is a lotic estuarine system that opens directly to the Gulf of Venezuela through the straits of Maracaibo. The most important river is the Catatumbo (27,809 km^2).

To the west the Tocuyo drainage (18,400 km^2) is of major importance. It has its origin in the northern flank of the Andes (3,585 m; Páramo de Cendé) and runs through a tectonic depression that eventually reaches coastal plains of fluvial-marine origin. The remaining orography is expressed by the Sierra of San Luis (1,400 m; Cerro Galicia), from which descend the Mitare (4,866 km^2), Hueque (5,642 km^2), and Ricoa (973 km^2) rivers and the Sierra of Aroa (c. 2,000 m), with the Aroa (2,450 km^2) and Yaracuy (2,565 km^2) rivers. Most rivers in arid Falcón state are intermittent *quebradas*, with dry beds during the period of drought.

The Coastal Mountain Ranges (length, 720 km) are divided into the Coastal (2,675 m; Pico Naiguatá) and Interior ranges (1,930 m; Cerro Platillón); between these two the endorheic drainage of Lake Valencia (3,140 km^2) exists in an elongate tectonic depression. The rivers of this central coastal region have very steep slopes and small drainages, and are of very short length (<25 km), except for the Tuy River (9,585 km^2). The continuation of the Coastal Mountain Range dominates the greater part of the eastern portion of the Caribbean slopes in trans-Andean drainages in NSA. The Turimiquire massif (2,596 m; Cerro Turimiquire) and the Serranía of Paria (1,350 m; Cerro Humo) are the major ranges of that region. The Turimiquire massif is drained in the north by short rivers that flow directly into the Caribbean Sea (Manzanares, Neverí) and to the east into the gulf of Paria (Atlantic drainage). Along the Paria peninsula the rivers are small and short (<20 km). The principal peak of Trinidad Island (4,828 km^2) is Aripo (940 m), and its rivers are all short.

FISH FAUNAS

The fish faunas of the Magdalena and Maracaibo drainages are composed of a mosaic of ancient relictual lineages along with new additions that have arrived through dispersal along the coast as well as endemic species that have evolved in isolation. Several authors have recognized the freshwater fishes of NSA as a distinct biogeographical unit (Eigenmann 1920; Schultz
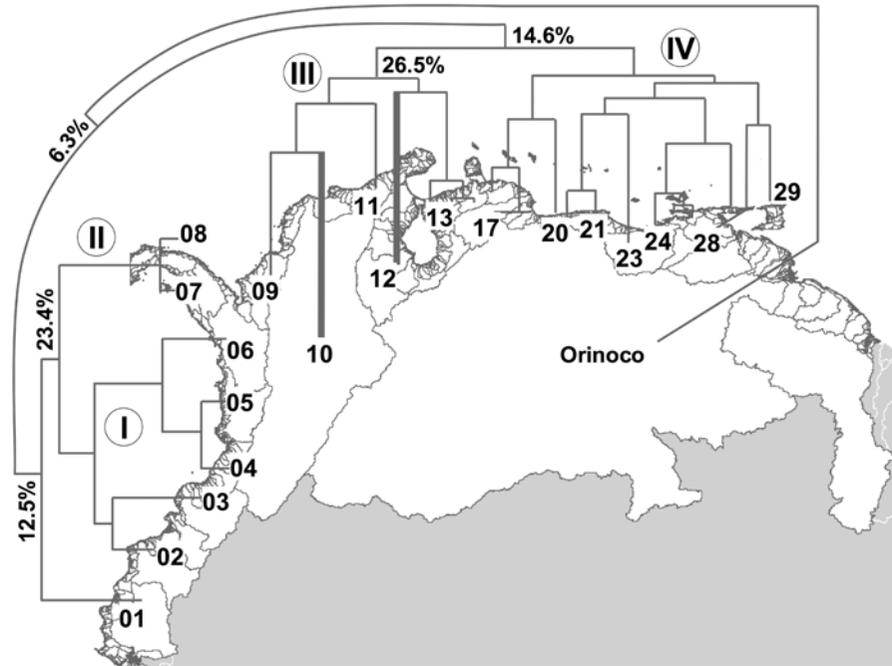
FIGURE 15.1 Relationships among fishes in the NSA and neighboring drainages based on the UPGMA dendrogram with the Jaccard coefficient (cophenetic correlation, 0.91). The drainages are Mira (01), Patía (02), Daguá (03), San Juan Pacific (04), Baudó (05), Atrato (06), Tuira (07), Chagres (08), Sinú (09), Magdalena (10), Ranchería (11), Maracaibo (12), Cocuiza, Maticora, and Mitare (13), Hueque, Tocuyo, Aroa and Yaracuy (17), Central (20), Tuy and Valencia (21), Unare (23), Neverí, Manzanares and Cariaco (24), Paria and San Juan Atlantic (28), and Trinidad (29). The principal units identified were Pacific Northern South America (I), Lower Mesoamerican (II), Magdalena (III), and Caribbean Northern South America (IV). The similarity between the fish faunas of the Magdalena and Maracaibo basins is 26.5%. For better visualization, some numbers have been omitted for a few drainages.

1949; Géry 1969; Mago-Leccia 1970; Dahl 1971). They also noted the high degree of similarity between the Maracaibo and Magdalena and commented on their relationships with the fish fauna of the Orinoco. The freshwater fish fauna is unique and diagnostic in these, as well as the lesser known cis-Andean drainages. The trans-Andean fish fauna has high species richness and endemism, and an ancestral relationship with the Amazon and Orinoco biotas; and for some families and genera, it represents the northern limit of their distributions. The relationship of the freshwater fish fauna of NSA with that of Lower Mesoamerica is long known and subject of much scientific comment. The emergence of the Isthmus of Panama and its importance as a passageway for dispersal and colonization of Central America by South American species is well known. S. Smith and Bermingham (2005) have estimated that processes of dispersal and colonization of lower Mesoamerica could have originated from both sides of the Andes, the Magdalena River, and the small Pacific drainages. The vicariant hypothesis presented by Carl Eigenmann has been supported by several fossils found in deltaic sedimentary deposits recording the presence of fishes that are no longer present in the area (e.g., *Phractocephalus*, *Colossoma*) but that are widely dispersed in the Orinoco and Amazon (Lundberg and Aguilera 2003; Dahdul 2004). A disjunct distribution has been observed for some groups (*Brycon*, *Rhinodoras, Potamotrygon,* and *Triportheus*), but for still others, extensive, widespread distributions seem to be the case (*Hoplias malabaricus*, *Astyanax fasciatus*). Small drainages with both very high species richness and endemism have been found, but most of these have depauperate fish faunas.

Faunal Records, Distribution, and Methods

DRAINAGE SELECTION AND FISH FAUNA RECORDS

We include here all coastal continental drainages between the Mira drainage and the Gulf of Paria, including the island of Trinidad in what we call Northern South America (NSA) (Figure 15.1). Based on biogeographic units proposed by Rodríguez-Olarte and colleagues (2009) the cis-Andean drainages in this work include all those drainages east of the Paraguaná peninsula (from Hueque to San Juan Atlantic, including those on Trinidad). We focus on drainages along the Caribbean slopes of NSA, principally Magdalena and Maracaibo. For comparison purposes we have also included some Caribbean and Pacific slopes of Lower Mesoamerica: the provinces of the Chagres and Tuira rivers, as defined by S. Smith and Birmingham (2005). We also include the Orinoco drainage as just one biogeographical unit. The grouping and division of drainages was established using the HydroSHEDS database (http://hydrosheds.cr.usgs.gov/), as well as relief, area, altitude, and drainage division maps (CIET 2005; Lehner et al. 2008).

The Pacific slope drainages were Mira, Patía, Dagua, San Juan (hereafter San Juan Pacific), Baudó, and Tuira. Included Caribbean slopes were Chagres, Atrato, Sinú, Magdalena, Ranchería, Maracaibo, Cocuiza, Matícora, Mitare, Hueque (including Ricoa), Tocuyo, Aroa, Yaracuy, Central (which contains several very small drainages), Tuy, Valencia, Unare, Neverí, Manzanares, and Cariaco. Atlantic slopes included Paria (with several small drainages of the Gulf of Paria), San

Juan (hereafter San Juan Atlantic), and the rivers of Trinidad. The coverage of fish samples is extensive and sufficient for us to assume that absences at the level of drainages, as here defined, are representative. We used records of freshwater fishes from the collections of CPUCLA, EBRG, ICN-MHN, MCNG, and MHNLS, andfrom the databases of California Academy of Sciences (http://www.calacademy.org), FishBase (Froese and Pauly 2008), and Sistema de Información sobre Biodiversidad de Colombia (http://www.siac.net.co). General and regional references were used to update the identification of these records when possible (e.g., Reis et al. 2003; Lasso et al. 2004; S. Smith and Birmingham 2005; Rodríguez-Olarte et al. 2009) and were supplemented with local reports, principally Mojica et al. (2004), Mojica, Castellano, et al. (2006), Mojica, Galvis, et al. (2006), Maldonado et al. (2006), Ortega-Lara et al. (2006a, 2006b), Rodríguez-Olarte et al. (2006, 2007), and Villa-Navarro et al. (2006).

Arbitrary epithets were included for those species without taxonomic description. We did not consider peripheral species that occurred mainly in marine environments or are amphidromous (e.g., Gobiidae, Ariidae and Gerreidae). For a few drainages, complete records of freshwater fishes do not exist. Taxonomic problems also hindered correct consideration of some species. Unique records were considered doubtful and were excluded if they were disjunct from the rest of the species. For some possibly valid species no records exist, and so they were recorded as present only from the type locality. Some species (e.g., *Hoplias malabaricus, Synbranchus marmoratus, Rhamdia quelen, Aequidens pulcher, Astyanax bimaculatus, Astyanax fasciatus, Poecilia reticulata*) have been reported from many drainages of Central and South America and are purported to have very wide distributions. We believe that eventually most of these will be shown to consist of groups of very similar species. In any case, the exclusion of these species from our analysis had no significant effects on the results reported here.

SPECIES RICHNESS AND DISTRIBUTIONS

Species richness of the principal groups of freshwater fishes was analyzed and the degree of endemism at the family, genus, and species levels was compared for the drainages within the study area. Fishes were also classified as either primary or secondary freshwater species, based on their tolerance to salinity (Stiassny and Raminosoa 1994). Primary freshwater species (e.g., Characiformes, Gymnotiformes) have no or very low tolerance to saltwater. Secondary freshwater species (e.g., Cyprinodontiformes, Perciformes) are tolerant to saltwater and, as such, have a greater potential for dispersal along stretches of coast devoid of freshwater outlets. To recognize the fundamental relationships between the number of species of fishes present and the surface area of a given drainage, different indices were calculated for comparison. To recognize the variation in species richness with respect to different mathematical models, we developed curves for the species-area relationship using both linear and power functions. In a species-area curve, high positive residual values suggest that the drainage has a species richness higher than the expected mean predicted by the model (Fattorini 2006). The model that best fits the data to the curve and the choice between the linear and the power function were determined using a corrected Akaike information criterion (AICc); in this manner it was possible to quantify the selection of the model that is most likely correct (Motulsky and Christopoulos 2003).

CLASSIFICATION AND ORDINATION

Multivariate classification methods are useful to discern biogeographic patterns exhibited by freshwater fishes. Matrices were elaborated for presence or absence of 33 strictly freshwater families of fishes (1,391 species and 414 genera). To characterize and compare relationships among the ichthyofaunas, cluster analyses were applied to classify them using the UPGMA algorithm and the Jaccard similarity coefficient (S. Smith and Birmingham, 2005). Cophenetic correlations were made to test natural groupings in the data (Rohlf and Fisher 1968). The cluster analyses were applied by means of the PC-ORD 4.25 software (McCune and Mefford 1999), and the cophenetic correlations with the PAST 1.80 program (Hammer et al. 2001). To contrast with classification, a non-metric multidimensional scaling analysis (NMS) was made using the Jaccard coefficient. The coordinates for NMS were generated by previous detrended correspondence analysis (DCA), and a test of goodness of fit for the determination coefficient (r^2) was carried out. The r^2 were generated in raw scale of the axes, but the graphics were ordered from minimum to maximum scale for better understanding; also, all ordination graphics were rotated for easier comparison. The drainages of the Paraguaná peninsula and Margarita Island were not included in the multivariate analyses because we did not have appropriate historical records.

BIOGEOGRAPHIC UNITS

To distinguish and characterize biogeographic entities we analyzed values of similarity obtained from the multivariate classification and ordination procedures. We consider endemic species as those restricted in distribution to just one drainage or province inside the study area. Those species that occurred in only borders of the study area (e.g., Mira drainage at the Colombia border with Ecuador, and San Juan Atlantic) were considered restricted because their general distribution was not determined for this study. The names of the biogeographic units were assigned following the guidelines of the International Code of Area Nomenclature (ICAN; Ebach et al. 2007). To select them, we used criteria proposed by Rodríguez-Olarte and colleagues (2009): Domains are considered extensive areas, like regional drainages or groups of drainages (e.g., Orinoco Basin) with homogeneous fish faunas that show very low similarity (usually less than 25%) with respect to neighboring entities. The provinces are medium-sized groups of drainages with faunas that have a similarity between 25% and 50%. Although in other studies we have identified subprovinces and territories within NSA (Rodríguez-Olarte et al. 2009), for this analysis those were not considered appropriate. The degree of endemism was also taken into consideration when designating boundaries between the drainages and biogeographical units.

Diversity, Shared Faunas, and Biogeographic Units

SPECIES RICHNESS, DISTRIBUTIONS, AND SHARED FAUNAS

In NSA, according to limits here established, we have documented the occurrence of 511 species of primary and secondary freshwater fishes. In Pacific and Atlantic slopes of Mesoamerica we recognized 55 species. The Pacific versants in NSA (Mira to Baudó drainages) contain 127 species, and the
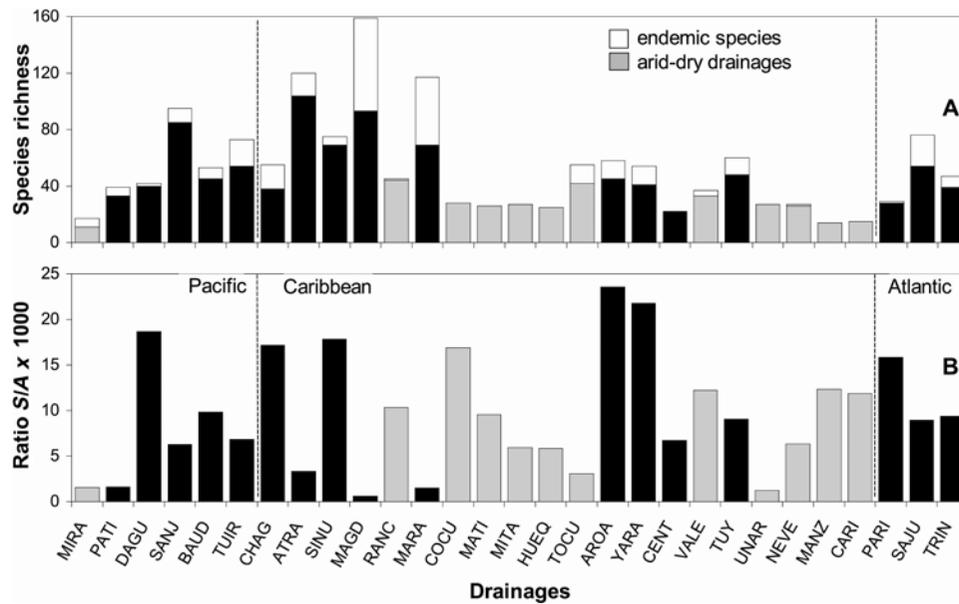
FIGURE 15.2 Variations of species richness of freshwater fishes in NSA drainages (except Orinoco). **A.** Variation in richness in true geographic sequence of the drainages. **B.** Species/area relationship [(S/A) × 1,000]. The drainages are Mira (MIRA), Patía (PATI), Daguá (DAGU), San Juan Pacific (SANJ), Baudó (BAUD), Tuira (TUIR), Chagres (CHAG), Atrato (ATRA), Sinú (SINU), Magdalena (MAGD), Ranchería (RANC), Maracaibo (MARA), Cocuiza (COCU), Maticora (MATI), Mitare (MITA), Hueque (HUEQ), Tocuyo (TOCU), Aroa (AROA), Yaracuy (YARA), Central (CENT), Valencia (VALE), Tuy (TUY), Unare (UNAR), Neverí (NEVE), Manzanares (MANZ), Cariaco (CARI), Paria (PARI), San Juan Atlantic (SAJU), and Trinidad (TRIN). The dashed lines separate modern divisions between the Pacific, Caribbean, and Atlantic slopes. Gray bars indicate dry to arid drainages that usually have lower species richness.

Caribbean slopes (Atrato to island of Trinidad) have 426 species. In Magdalena and Maracaibo drainages we documented 246 species. In terms of orographic classification we recorded 306 species from strictly trans-Andean drainages (from Mira to Mitare drainages), which is about 73% of the total. In the cis-Andean drainages (from Hueque to San Juan Atlantic drainages, including Trinidad) 169 species occur, and 93 of them are found only in those drainages. Among Pacific drainages, the San Juan Pacific drainage has the highest number of species (95 spp., 10 endemic), and in Caribbean drainages those with the most species were Magdalena (159 spp., 66 endemic), Atrato (120 spp., 19 endemic), and Maracaibo (115 spp., 48 endemic), all located in humid regions. The rest of the rivers draining into the Caribbean or the Atlantic have relatively low diversity with the exception of a few originating in the Coastal Cordillera such as Aroa (59 spp.), Tuy (60 spp.), and San Juan Atlantic (76 spp.), which flows into the Atlantic near the Orinoco Delta. Drainages with higher fish biodiversity are separated by smaller coastal rivers with much lower species richness, which usually originate in very arid regions such as those along the coast of Falcón state or the Guajira peninsula (Figure 15.2A).

The Magdalena and Maracaibo basins share 28 species, of those, 24 are exclusives; that is, they occur only in those drainages (Table 15.1). The Magdalena shares fewer species with the Orinoco (14 spp.; 9 exclusives) than the Maracaibo Basin. Very few species were common to all three basins—*Astyanax fasciatus*, *Eigenmannia virescens*, *Hoplias malabaricus*, *Parodon suborbitalis,* and *Synbranchus marmoratus*—and we suspect that ongoing taxonomic revisions will reveal that in fact even these are not really the same species in all three. In NSA several genera are restricted to trans-Andean drainages (Figure 15.3), including *Caquetaia, Ctenolucius, Crossoloricaria, Saccoderma, Gilbertolus, Ichthyoelephas, Cheirocerus, Doraops, Eremophilus,* and *Genycharax.* Among the strictly trans-Andean genera sev-

eral are endemic to the Magdalena Basin (*Centrochir, Genycharax, Grundulus*) or Maracaibo (*Doraops, Perrunichthys*). Several genera have a disjunct distribution: occurring in the Orinoco and the trans-Andean drainages but not in the Caribbean NSA domain (e.g., *Brycon*, *Sturisoma*, *Geophagus*, *Astroblepus*, *Hemiancistrus*, *Lebiasina,* and *Ageneiosus*, among others). Of the genera that are not reported outside of the cis-Andean drainages we find *Crenicichla*, *Aphyocharax*, *Corynopoma*, *Corydoras*, *Ctenobrycon*, *Microglanis,* and *Loricariichthys*, among others.

In humid drainages there are proportionally more primary species (c. 65%), than in arid regions where secondary fishes dominate and can reach 50% of the total species present. There are, however, exceptions to this generalization, such as the Tocuyo and the Unare rivers, where overall richness is low relative to the size of the watersheds. A cluster analysis applied only to genera revealed a possible artifact of the classification model (Figure 15.4): the recognition of the climatic condition of the drainage by taking into consideration the type of fish taxa present. In the cluster analysis the trans- and cis-Andean drainages were discriminated in a general way, but the majority of arid and dry drainages where secondary species predominate clustered together.

The density of taxa per unit area showed significant variation, but the general tendency is to diminish in function with an increase of drainage surface area: larger drainages had more species and usually lower density with respect to smaller drainages. The small drainages of Aroa and Yaracuy have very high densities of more than 20 species per 1,000 km^2. Indeed, we determined that the Aroa and Yaracuy drainages had the highest species richness per unit area of all NSA. Together, these drainages, with some 4,944 km^2 (about 0.9% of the total area studied) contain about 10.3% of all species present in NSA (Figure 15.2B). Small drainages like the Cocuiza also had elevated values of species density, having just a few species in a very small area. In contrast, the Magdalena Basin with 256,622

TABLE 15.1
Freshwater Fishes Shared among the Magdalena, Maracaibo, and Orinoco Basins

Families	Magdalena/Maracaibo	Magdalena/Orinoco	Maracaibo/Orinoco
Cichlidae	*Aequidens pulcher*		
	Caquetaia kraussii		
Anostomidae		*Leporellus vittatus*	
		Leporinus striatus	
Characidae	*Astyanax fasciatus*	*Astyanax bimaculatus*	*Astyanax fasciatus*
	Astyanax magdalenae	*Astyanax fasciatus*	*Bryconamericus loisae*
	Gephyrocharax melanocheir	*Astyanax microlepis*	*Roeboides dientonito*
	Nanocheirodon insignis		
Ctenoluciidae	*Ctenolucius hujeta*		
Crenuchidae			*Characidium chupa*
			Characidium boaevistae
Erythrinidae	*Hoplias malabaricus*	*Hoplias malabaricus*	*Hoplias malabaricus*
Gasteropelecidae	*Gasteropelecus maculatus*		
Lebiasinidae			*Piabucina erythrinoides*
Parodontidae	*Parodon suborbitalis*	*Parodon suborbitalis*	*Parodon suborbitalis*
Poeciliidae	*Poecilia caucana*		*Poecilia reticulata*
Rivulidae	*Rachovia brevis*		
	Rachovia hummelincki		
Auchenipteridae	*Ageneiosus pardalis*		
Astroblepidae	*Astroblepus chotae*	*Astroblepus frenatus*	
Aspredinidae	*Dupouyichthys sapito*		
Callichthyidae	*Hoplosternum magdalenae*		*Megalechis thoracata*
Heptapteridae	*Imparfinis nemacheir*	*Cetopsorhamdia molinae*	
	Rhamdia guatemalensis		
Loricariidae	*Dasyloricaria filamentosa*	*Chaetostoma milesi*	
	Hypostomus hondae		*Ancistrus triradiatus*
	Rineloricaria magdalenae		*Chaetostoma tachiraense*
	Sturisomatichthys leightoni		*Hypostomus watwata*
Pimelodidae	*Sorubim cuspicaudus*		
Hypopomidae			*Brachyhypopomus occidentalis +*
			B. pinnicaudaus
Gymnotidae		*Gymnotus ardilai + G. carapo*	
Sternopygidae	*Eigenmannia virescens*	*Eigenmannia virescens*	*Eigenmannia virescens*
Sternopygidae		*Eigenmannia humboldti + E. limbata*	
Sternopygidae	*Sternopygus aequilabiatus + S. pejeraton*		*Distocyclus goajira + D. conirostris*
Apteronotidae	*Apteronotus rostraus*		
Apteronotidae	*Apteronotus magdalenensis + A. cuchillo*		*Apteronotus cuchillejo + A. albifrons*
Potamotrygonidae	*Potamotrygon magdalenae*		
Synbranchidae	*Synbranchus marmoratus*	*Synbranchus marmoratus*	*Synbranchus marmoratus*

NOTE: Cis-Andean Caribbean drainages are not included (Western, Central, and Eastern Caribbean provinces). Some species with putatively widespread distributions are species complexes in need of taxonomic revision.

km²; which is 49% of the total study area, has only 0.62 species per 1,000 km² and a richness of only 29% of the total number of species of NSA.

Drainage area is positively correlated with the number of species present. The linear function model for species-area relationship for the drainages of NSA showed better fit than the power function ($S = 37.87 \times 0.00083(A)$; $R^2 = 0.97$), and showed a robust Akaike differential (ΔAICc = 25.86; >99.9%). When the Orinoco is excluded, the power model is best ($S = 2.697 \times A^{0.3288}$; $R^2 = 0.63$; ΔAICc = 8.32; 98.5%; Figure 15.5); although its explicative ability was lower. Upon removal of the third-largest drainage in surface area (Magdalena), the explicative ability diminishes considerably and in that case there was no evidence (ΔAICc = 0.16; 51.9%) favoring one model over another. Thus the second model was selected as best representing the species-area relationships in NSA. Among the major drainages with largest deviations of posi-

tive residuals were Atrato, Sinú, San Juan (Atlantic and Pacific slopes), and Aroa. These can be considered as having elevated species richness. In contrast, the species-area relationship calculations were sensitive to drainages with low species richness with respect to the curve, principally Unare, Mira, Patía, and Hueque drainages. These drainages are characterized by dry to arid climates. Drainages with similar species richness to those predicted by the model include Trinidad, Ranchería, Valencia, and Magdalena.

FAMILIES AND THEIR DIVERSITY GRADIENTS

Among the 33 families found, the Characidae (157 spp.) and Loricariidae (102 spp.) contributed almost half (51%) of total species richness in NSA and, while significant in all drainages, were particularly abundant in the larger drainages of Magdalena, Maracaibo, and Atrato. Other important families were

Figure 15.3 header:

Genera	Pacific NSA	MAG	MAR	Caribbean NSA	O

Caquetaia
Ctenolucius
Crossoloricaria
Saccoderma
Sturisomatichthys
Argopleura
Leptoancistrus
Priapichthys
Saccodon
Gilbertolus
Phenagoniates
Dupouyichthys
Ichthyoelephas
Carlastyanax
Centrochir
Cheirocerus
Doraops
Eremophilus
Genycharax
Grundulus
Perrunichthys
Rhinodoras
Tridensimilis
Brycon
Sturisoma
Geophagus
Astroblepus
Hemiancistrus
Lebiasina
Ageneiosus
Dasyloricaria
Imparfinis
Cynopotamus
Dolichancistrus
Spatuloricaria
Crenicichla
Aphyocharax
Corynopoma
Corydoras
Ctenobrycon
Microglanis
Loricariichthys
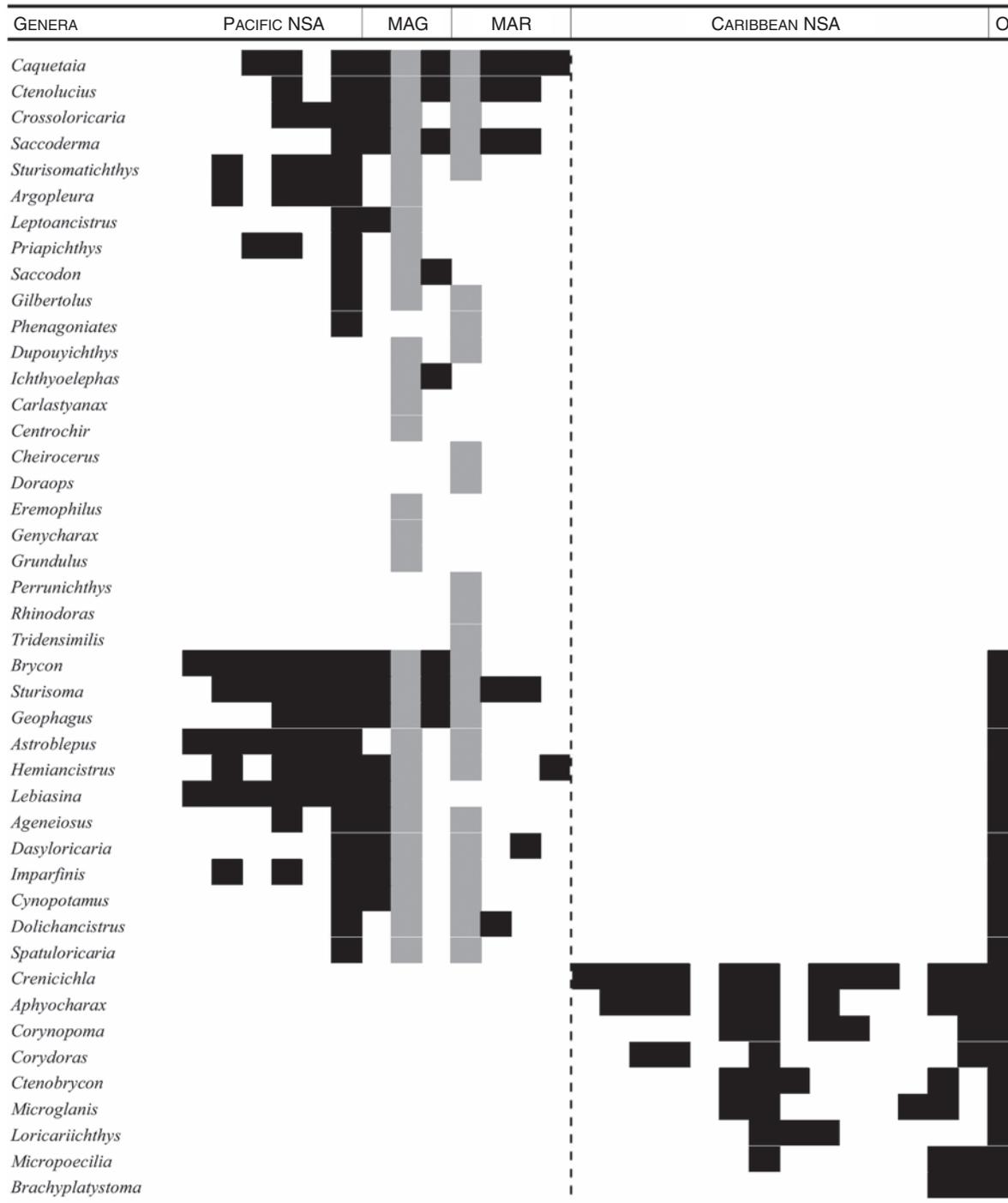Micropoecilia
Brachyplatystoma

FIGURE 15.3   Distribution of several common genera within NSA. Pacific NSA and Caribbean NSA are dominions. MAG and MAR are the Magdalena and Maracaibo provinces. O, Orinoco. Within each biogeographic unit the occurrence of genera in each drainage is shown. The dashed line separates trans- and cis-Andean drainages.

Cichlidae and Trichomycteridae (30 spp.; 5.9%), Poeciliidae (26 spp.), Heptapteridae (24 spp.), Astroblepidae (23 spp.), and Rivulidae (23 spp.; 4.5%). Taken together, these families make up about 74% of all species known from NSA. For the Characidae the greatest number of species is found in the Magdalena Basin (45 spp.), followed by the Atrato (39 spp.), San Juan Pacific (24 spp.), Chagres (23 spp.), Sinú, and Tuy (22 spp. c/u). The Loricariidae family reach their highest numbers in the Maracaibo drainage (27 species), highest of all studied drainages of NSA both in absolute numbers and proportion of the total. Next for Loricariidae we have the Magdalena (22 spp.) and the Atrato (19 spp.). The distribution of Cichlidae in NSA shows more species in the Pacific drainages of Colombia (12 spp.) and from the Isthmus of Panama (9 spp.). The family Ctenoluciidae has two species: *Ctenolucius beani* in Pacific slope drainages and *Ctenolucius hujeta* in Caribbean versants (Magdalena and Maracaibo), while the stingrays (Potamotrygonidae) have two species in the Maracaibo basin and one in Magdalena, but are absent from Pacific and Lower Mesoamerican drainages.
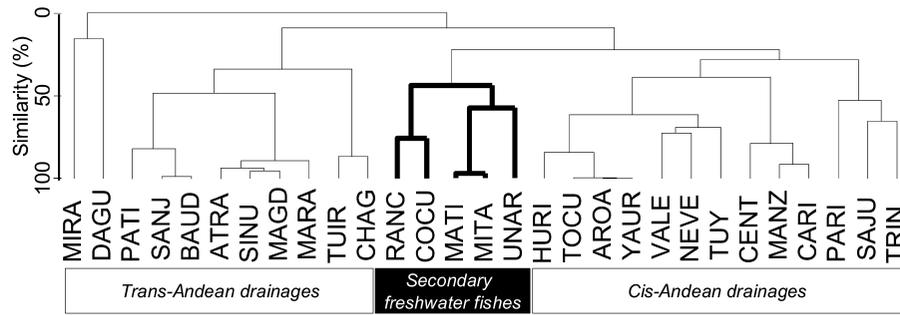
12

FIGURE 15.4   UPGMA classification algorithm using the Jaccard coefficient for genera of freshwater fishes in NSA (cophenetic correlation, 0.83). The majority of the arid drainages, where secondary freshwater fishes prevail, were grouped whether or not they are trans- or cis-Andean. The Ranchería drainage is trans-Andean, and the Unare is cis-Andean.
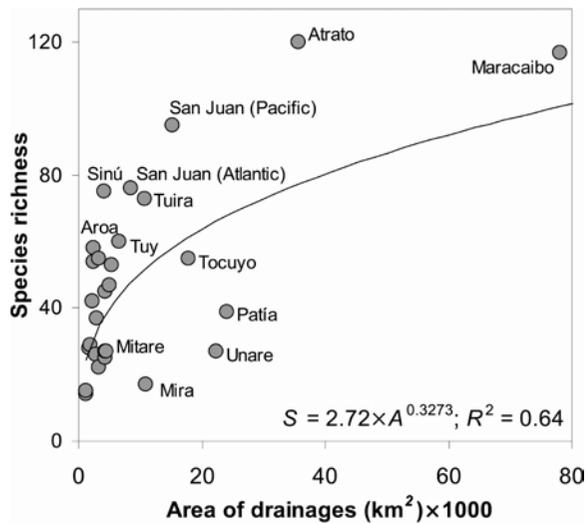

FIGURE 15.5   Species-area relationships plotted on a curve adjusted using the power function. The power model was chosen based on robust values of Akaike differential (ΔAICc = 8.087; ~98.28%). The deviation from the mean of this model suggests the existence of drainages with elevated (e.g., Atrato) as well as very low (e.g., Unare) species richness with relation to drainage size. The very large Magdalena Basin is not shown, for reasons of scale.
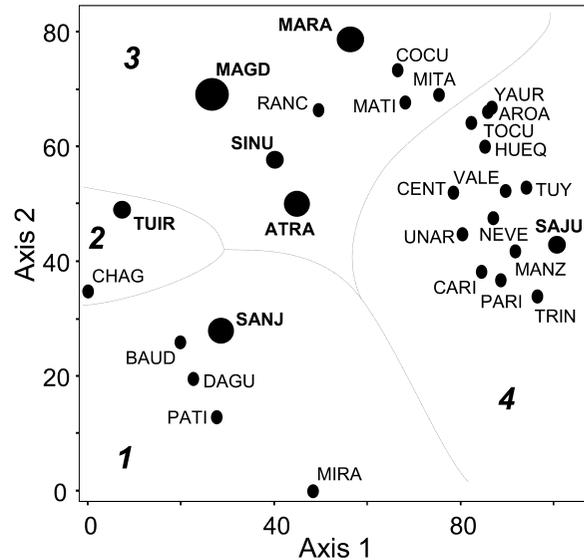

FIGURE 15.6   Ordinations from nonmetric multidimensional scaling (NMS) analysis, based on the UPGMA algorithm and Jaccard coefficient ($r^2 = 0.58$; orthogonality = 98%; stress = 20.1).The ordination was rotated for visual purposes. The arrangement of all basins is related to their true geographical sequence. The biogeographical domains were moderately separated: Pacific (1), Lower Mesoamerican (2), Magdalena (3), and Caribbean (4). The drainages with high species richness are indicated by larger symbols. The Orinoco Basin was excluded for reasons of scale.

Species richness decreases toward the east in NSA but increases again in the easternmost drainages of Venezuela, where genera typical of the Orinoco occur (*Crenicichla*, *Apistogramma*, and *Astronotus*). The family Trichomycteridae shows its greatest diversity in the Magdalena, with 11 nominal species of *Trichomycterus* and two endemics: *Eremophilus mutissi* and *Paravandelia phaneronema*. The other drainages of importance for this family were the San Juan Pacific (5 spp.) and Maracaibo (4 spp.). The high-mountain astroblepid catfishes have a mostly trans-Andean distribution and reach their highest diversity in the Magdalena (15 species) and rivers in Pacific drainages of Colombia, like San Juan Pacific and Dagua (12 and 10 spp.). In the Dagua River, nominal species of astroblepid catfishes comprise 24% of all the fishes known from the drainage. In the Maracaibo drainage only one species is thought to be present. Astroblepid catfishes are absent from the rivers of Lower Mesoamerica and the Caribbean slopes of Venezuela, as well as from the Sinú and Rancheria drainages. The Gymnotiformes are dominated by the families Apteronotidae (17 spp.) and Sternopygidae (12 spp.) and showed more diversity in Magdalena (9 spp.) and San Juan Pacific (8 spp.) drainages, while in Atrato, Sinú, and Maracaibo seven species are

recognized. In the rest of the drainages the richness of electric fishes does not surpass three species.

CLASSIFICATION AND ORDINATION

The arrangement of the NSA drainages based on our analysis of species presence-absence shows that the clusters generated were similar overall to their real geographic positions (Figure 15.1). A high cophenetic correlation ($r = 0.91$) indicated that the records used for the construction of the UPGMA dendrogram had adequate fit, and that our NMS ordinations were both adequate and robust ($r^2 = 0.58$; orthogonality = 98%; stress = 20.1; Figure 15.6). The relationships between the fish faunas showed two large clusters, considered here as the NSA, and the Lower Mesoamerican subregions. These subregions have very low similarity (c. 6%) between them at the species level. At the second hierarchical level with high similarity we recognized the following domains: Pacific NSA, Lower Mesoamerica, Magdalena, and Caribbean NSA. These domains show

TABLE 15.2

Biogeographic Units Recognized within NSA and Neighboring Drainages According to
the Results of Classification and Ordination Analyses

By Drainage: Total Number of Families (F), Genera (G), Species (S), and Endemic Species (S_E).

Dominion	Provinces	Drainages	A (km²)	F	G	S	S_E
Pacific Northern South America	1. Patía	Mira[a]	10,901	8	11	17	6[e]
		Patía	24,000	14	28	39	6
		Dagua	2,250	12	23	42	2
	2. Atrato	San Juan Pacific	15,180	24	50	95	10
		Baudó	5,400	17	38	53	8
		Atrato[b]	35,702	29	73	120	19
Lower Mesoamerica	3. Tuira	Tuira	10,664	21	54	73	17[e]
	4. Chagres	Several drainages	3,206[c]	11	33	55	16[e]
Magdalena	5. Magdalena	Sinú	4,200	24	56	74	6
		Magdalena	256,000	31	87	159	66
		Ranchería	4,347	21	41	46	1
	6. Maracaibo	Maracaibo	78,180	29	82	115	48
		Cocuiza	1,660	13	26	28	—
		Maticora	2,713	11	24	27	—
		Mitare	4,535	10	20	26	—
Caribbean Northern South America	7. Western Caribbean	Hueque	4,272	9	20	25	—
		Tocuyo	17,854	16	35	56	13
		Aroa	2,463	18	36	58	13
		Yaracuy	2,481	17	34	55	13
		Central	3,274	9	15	22	—
	8. Central Caribbean	Valencia	3,024	11	26	36	4
		Tuy	6,606	17	45	60	12
		Unare	22,318	13	24	27	0
		Neverí	4,281	11	23	26	1
		Manzanares	1,135	7	12	14	0
		Cariaco	1,260	8	12	14	0
	9. Eastern Caribbean	Paria	1,828	14	27	28	1
		San Juan Atlantic	8,506	23	60	75	22[e]
		Trinidad	4,996	17	40	47	8
Orinoco[d]	—	Several drainages	~1,000,000	77	367	941	

[a]The Mira drainage was not included in any biogeographic unit because it is on the border of the study area.

[b]The Atrato River today empties into the Caribbean.

[c]Corresponds to the Kuna Yala comarch in Panamá.

[d]The designation Orinoco domain is suggested.

[e]Considered not endemic, only restricted.

very low similarity (12–15%) and group units defined by nine biotas that correspond to the following provinces (listed here in geographic sequence from Pacific to Atlantic): Patía (1), Atrato (2), Tuira (3), Chagres (4), Magdalena (5), Maracaibo (6), Western Caribbean (7), Central Caribbean (8), and Eastern Caribbean (9).

BIOGEOGRAPHIC UNITS

The biogeographic patterns taken into consideration show the confluence of four large biotas in NSA: Pacific, Mesoamerican, Caribbean, and Atlantic (Table 15.2). In the Caribbean NSA

domain (103 spp.; 46 endemics) the three provinces identified show important differences: the Western Caribbean province has the largest number of endemic species (23.3%), and its richness is the lowest of the domain (73 spp.). Species richness for the Central Caribbean province is higher, and reaches 87% of all the species present in the domain with 16.1% endemism. The extreme edge of the Caribbean biotas is the Eastern Caribbean province, which includes Atlantic drainages: Paria, San Juan Atlantic, and Trinidad. In this province there is an important interchange with fishes of the Orinoco Basin, which shares about 12.9% of its fish fauna with drainages of NSA, mostly with the Caribbean NSA domain. The number of
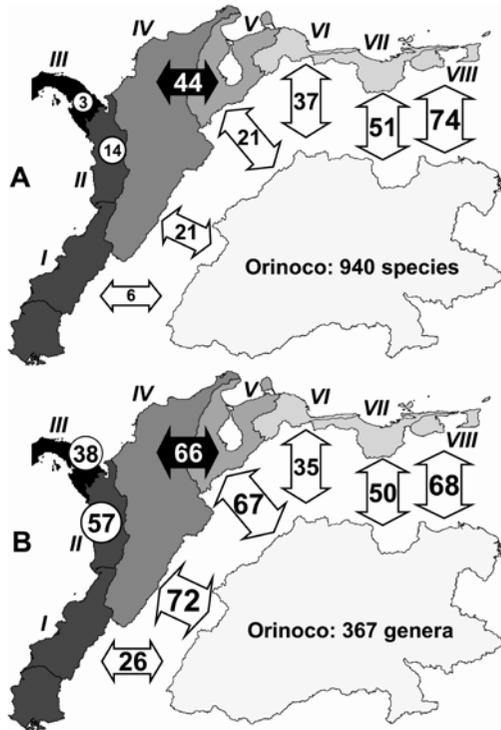
FIGURE 15.7   Species (A) and genera (B) shared among the recognized biogeographic provinces and the Orinoco Basin: Patía (I), Atrato (II), Lower Central America (III: Tuira and Chagres provinces), Magdalena (IV), Maracaibo (V), Western Caribbean (VI), Central Caribbean (VII), and Eastern Caribbean (VIII).

species shared with other biogeographic units diminishes dramatically from east to west (Figure 15.7). The Orinoco shares 74 species (7.9%) with the drainages that empty into the Atlantic to the north (Eastern Caribbean province), but with the drainages of the Falcón coast (Western Caribbean province) there are only 38 species in common. With the Maracaibo and Magdalena the number drops to 22 and 21 shared species, respectively, but with the Pacific drainages there are many fewer, only 14 species in the Atrato and 6 species with the Patía.

Provinces, Faunas, and Drainages

SPECIES RICHNESS, DISTRIBUTIONS, AND SPECIES-AREA RELATIONSHIPS

The distribution of freshwater fishes in NSA shows a robust correlation with the principal geographic and climatic aspects of the region based on our analyses of species occurrence, richness, and endemism. The most important taxa shared between the Magdalena and Maracaibo drainages, 23 genera and 27 species, are presented in Table 15.1 and Figure 15.3. The high similarity of the fish faunas of these drainages suggests a common origin or at least an ancestral connection between them that has permitted the mixing of their fishes, as has been noted by several authors (Eigenmann 1905; Pérez and Taphorn 1993; Lundberg et al. 1998; Albert et al. 2006). Our analyses determined that the number of species in common between the Magdalena, Maracaibo, and Orinoco basins differs as follows: Magdalena-Maracaibo: 32 spp.; Magdalena-Orinoco: 16 spp.; Maracaibo-Orinoco: 21 spp.

We expected to find that more lowland floodplain species, as well as secondary species that have a higher potential for dispersal along marine coasts, would be held in common, but that is not the case. Rather, we find that the Magdalena and Maracaibo basins share a mixture of genera and species from all altitudes. Analysis of distribution records indicates that several families are shared, represented for the most part by fishes of small size, that the majority inhabit floodplain or piedmont regions, except for the astroblepids (but this family is currently undergoing taxonomic revision, and we expect many changes in the alpha-level identifications that would directly effect our interpretations of their distributions). Many of the other species in common include species complexes. The supposed very widespread distributions of *Astyanax fasciatus, Hoplias malabaricus,* or the *Sternopygus aequilabiatus* complex (Hulen et al. 2005), for example, that have been reported from almost all the drainages of the NSA coast as well as the Orinoco Basin, will be revealed as the adjacent occurrence of very similar sister species as taxonomic and phylogenetic studies of these groups advance. Once these species complexes have been resolved, we believe that the similarities of the fish faunas of the Magdalena, Maracaibo, and Orinoco basins will be further reduced.

Some nominal species (e.g., *Leporellus vittatus* Anostomidae, *Sternopygus macrurus* Sternopygidae) seem to be present in both trans- and cis-Andean drainages, hinting at the existence of an ancestral, common NSA watershed. Assuming that generic identifications are more accurate, an analysis of similarity at this level may suggest more reliable estimates of relationships between the drainages (Albert et al. 2006). Some genera (e.g., *Cheirocerus*, *Gymnotus*, *Rhinodoras*, and *Tridensimilis)* have very widespread distributions that include all of NSA and also occur as far away as the Amazon and Paraná basins, a finding which suggests very old watersheds uniting most of South America (see Chapter 1). Other genera have only trans-Andean distributions that imply they have evolved in situ (e.g., *Caquetaia*, *Ctenolucius*, *Argopleura*, *Saccodon*, *Gilbertolus*, and *Genycharax*). Many genera are present only in cis-Andean drainages (e.g., *Apistrogramma*, *Aphyocharax*, *Brachyplatystoma*, *Corydoras*, *Ctenobrycon*, *Crenicichla*, *Microglanis, Sternarchorhynchus*) and are widespread throughout the Amazonas and Orinoco basins. The absence of these taxa from trans-Andean portions of NSA does not necessarily mean that they have been lost to extinction; some may have originated after the mountains arose to separate the drainages into cis- and trans-Andean components. Many genera are shared by the trans-Andean and Orinoco drainages, but do not occur in the Caribbean domain (*Ageneiosus*, *Astroblepus*, *Brycon*, *Cynopotamus*, *Geophagus*, *Sturisoma*, etc.); these disjunct distributions suggest extirpation from the Caribbean domain, which may be due to multifactor variables linked with species-area effects, aridity, marine incursions, or altitude.

Species density varies a great deal in NSA (Figure 15.2B). We believe that the occurrence and sequence of geological and climatic parameters are the causes of the observed extreme variation. Density as an attribute of biodiversity has natural limitations because it is expressed in units of area. Extremes of density can be found in either small or large drainages. The values found here indicate that the small, dry drainages can have elevated densities (Cocuiza: 16.9 spp./1,000 km^2), comparable with drainages of high species richness (Aroa: 23.5 spp./1,000 km^2). The Magdalena Basin (0.62 spp./1,000 km^2) has much lower density than that recorded for the Maracaibo Basin (1.5 spp./1,000 km^2). Examples of great variability are common: the Amazon, with a watershed of around 7,000,000 km^2,

is still very poorly surveyed, and estimates vary greatly from 1,500 to 5,000 species. This works out to between 0.21 and 0.71 species per 1,000 km². Taking a middle range number of 2,500 species for the Amazon would yield 0.36 species for every 1,000 km² of drainage area. The better but still incompletely surveyed Orinoco, with approximately 1,000,000 km², has around 1,000 described species (Lasso et al. 2004), or 1 species per 1,000 km². The much larger but mostly subtropical Paraná River with c. 3,000,000 km² has only 600 species reported (Bonetto 1986) and a low ratio of species/area at 0.20 species per 1,000 km². So for species-density ratios, along the coast of NSA, the larger basins do not necessarily have more species of freshwater fishes.

The species-area functions are often used without due consideration of the optimum model that has more sensitivity or that might better explain the relationship in drainages of different sizes. Consensus for an optimum function for species-area relationships has not yet emerged, in part because no one function will always reflect the best biogeographic arrangement or detect ecological patterns (Scheiner 2003). Besides drainage area, the geologic history and climatic conditions, as well as habitat gradients that are a result of these, are fundamental elements of any biogeographic model. The increase in the number of species with regard to an increase in drainage area is evident as an overall parameter, but other factors can notably affect this relationship. The surface area of the drainages can influence the adjustment curve; differences vary significantly with respect to drainage size, as in the case of the Aroa (2,463 km²) and Orinoco (c. 1,000,000 km²), which have direct influence on the species-area models, principally because different functions have different sensitivities according to the interval of the areas used. This should be a warning about the use of species-area models and shows that it is a good idea to test different functions. In NSA, climate may better explain why some drainages of intermediate size have important deviations in their species-area relationships when using the power function model, as has been shown for drainages along the Venezuelan coast (Rodríguez-Olarte, unpublished data). This result is associated with changes in the Pleistocene of NSA and is a product of the latitudinal displacement of the Intertropical Convergence Zone and sea-level changes (González et al. 2008) that have caused the desertification of some drainages and decimated the fish fauna. For example, the Unare river drainage currently has very low species richness even though its size is much greater than many small coastal drainages with more species.

BIOGEOGRAPHIC PROVINCES

The results of our classification and ordination permit the recognition and designation of biogeographic units for which species richness, fish distribution patterns, and location correlate with modern orographic features, and to varying degrees with the geological and ecological history of NSA. In NSA the biogeographic units strictly correspond to freshwater fish faunas, extending and discriminating further the units previously recognized by various authors such as Géry (1969), who recognized for these fauna a larger unit (Orinoco-Venezuelence) made up of the provinces of the Lake Maracaibo Basin, the Caribbean Coast, Orinoco, and Trinidad. At an even wider scope, Morrone (2001) considered that for NSA the Chocó, Magdalena, Maracaibo, Venezuelan Coast, and Trinidad and Tobago should be recognized as one unit. Robin and colleagues (2008) presented a detailed classification of freshwater

ecosystems that for NSA is very similar to ours. Recently, Rodríguez-Olarte and colleagues (2009) recognized various biogeographic units for the Venezuelan coast; using that classification scheme, we describe the following units:

PATÍA AND ATRATO PROVINCES (PACIFIC NORTHERN SOUTH AMERICA DOMAIN)

Two provinces were identified by similarity analysis for the fish faunas of the Colombian Pacific region (Figure 15.1). The first is the Atrato River (Caribbean slope) along with the Baudó and San Juan (both on the Pacific slope), and the other is made up of the Dagua and Patía rivers, which are very similar to one another, along with the Mira River, which has a very reduced fish fauna and may possibly be more similar to rivers of Pacific Ecuador. These results indicate affinities opposite to those found by J. Mojica and colleagues (2004), who considered that the fishes of the Atrato were more similar to those of neighboring Magdalena. It is likely that interchanges of fishes still are occurring, as was noted by Eigenmann (1920) many years ago. In the region of the Isthmus of Panama the dividing lines between the waters of the Atrato, Baudó, and San Juan Pacific are within 10 km of each other in a low-altitude region (200 m). It may be supposed that before the uplift of the Darien mountain range, the Atrato River emptied into the Tuira Gulf on the Pacific slope of Panama. This is suggested by the large size of the Tuira River delta, which is disproportionate for a river of its size. This also would explain the high proportion of species shared between the Atrato and the Pacific drainages. The Mira and Patia rivers have fewer than expected species for their drainage areas (Figure 15.5). Perhaps, like other Pacific drainages, they have been influenced by aridity, a characteristic of Peruvian and Ecuadorian coastal drainages further south. The small San Juan Pacific river is a notable exception for the region, having relatively high values on the species-area curve, probably because of the high rainfall and humid conditions of the drainage that produce an unusually large flow in this river. The current poor state of knowledge of the region's fish fauna makes it difficult to analyze true endemism present in these drainages. Species that we now list as endemic may prove to be present in neighboring drainages once sampling is possible. Even though conditions are humid and the rivers have high flows, the fish diversity is much less notable than that recognized for other groups such as plants or amphibians; in addition, fishery resources are very limited, and small species like *Brycon* and *Cichlasoma* are important in local fisheries. In the area where the Isthmus of Panama joins with NSA (the Chocó biogeographic unit) the fish faunas of Central America, Magdalena, and the Orinoco converge.

CHAGRES AND TUIRA PROVINCES (LOWER MESOAMERICA DOMAIN)

Even though the Chagres and Tuira provinces have a considerable similarity with respect to the Pacific versant of NSA, their fish faunas belong to separate biotas, as has recently been shown (S. Smith and Bermingham 2005). Cichlids, poeciliids, and characids have high species richness in these provinces. Both provinces are closely related, both in the past and today, with the fish faunas of eastern NSA: Chagres shares around 25% of its fishes with the Atrato drainage, and Tuira has about 40% in common. A general consensus holds that NSA was the source of fishes that colonized Mesoamerica thanks to the uplift of the Isthmus of Panama in the Pliocene and the

opening of colonization routes (G. Myers 1966; Reeves and Bermingham 2006). The fish fauna of the Tuira province has a low similarity with that of the Atrato, suggesting rapid speciation and/or extinction associated with the orogeny of the mountains separating these basins.

MAGDALENA AND MARACAIBO PROVINCES (MAGDALENA DOMAIN)

Ichthyological affinities among the Magdalena, Maracaibo, and Orinoco drainages have been recognized by several authors (Eigenmann 1920; Schultz 1949; Pérez and Taphorn 1993). Fossils found in the upper Magdalena River valley (*Arapaima*, *Colossoma*, *Lepidosiren*, *Phractocephalus*) ratify the existence of an ancestral biota that occupied the paleodrainages that today have divided into the Amazon and Orinoco basins (Lundberg et al. 1998). The only species of great body size that survives today is of cis-Andean origin and occurs in the Magdalena drainage: the predatory tiger catfish *Pseudoplatystoma magdalenatum* (c. 100 cm length). This is a genus of ample distribution in the great South American drainages of the Amazon, Orinoco, and Paraná, and the Magdalena drainage is its northern limit. This genus is absent from the Maracaibo basin. It is, perhaps, the only species of great size to survive the extensive geological and climatic changes that have occurred in NSA. This type of distribution pattern is also known for other genera and families. One species of doradid thorny catfish, *Centrochir crocodili*, is present in the Magdalena drainage, and two are in the Maracaibo (*Doraops zuloagai* and *Rhinodoras thomersoni*). These are the only species present in Caribbean drainages of these abundant and diverse Amazonian and Orinocoan families.

In the Magdalena drainage and associated rivers the prochilodontids are of biogeographic interest: *Prochilodus magdalenae*, a migratory species, occurs throughout the drainage, from mountains to floodplains to complete its life cycle. The elephant-nosed prochilodontid, *Ichthyoelephas,* lives in piedmont streams of the Magdalena Basin, but also occurs in the Guayas River, of the Pacific slopes of Ecuador. This disjunct distribution is linked to the ancient connections of these drainages. Even though species richness in Andean rivers diminishes rapidly with increasing elevation, the upper Cauca, a major Magdalena tributary above 900 m, is a region of relatively high fish species diversity (70 spp.; 14 endemics; Ortega-Lara et al. 2006a). The conditions of the high valley, together with its isolation from the rest of the drainage by extensive rapids of nearly 200 km in length, have caused variable isolation of the highland species confined there (Maldonado-Campo et al. 2005). The high reaches of the Eastern Cordillera, in spite of their high elevations (2,500–2,800 m), are also distinguished as an enclave of high species richness and endemism; this tributary is completely isolated by the Tequendama Waterfall (a 300 m drop). At least three monotypic genera are restricted to the high plains of Bogotá: *Grundulus* (Characidae), and *Eremophylus* and *Rhizosomychthys* (Trichomycteridae). The presence of these unique genera there is due to the extreme geographic isolation of the high plains. As has been already noted, montane genera (e.g., *Astroblepus* and *Trichomycterus*) are very diverse in the Magdalena Basin. Many species of these families are still poorly known taxonomically, and revisions will undoubtedly uncover even more new species.

About 21% of the freshwater fishes of NSA occur in the Maracaibo province. Some primary freshwater species have disjunct distributions with other provinces that could be explained by regional geological history. The Limón River drainage (at the northwest edge of the Maracaibo Basin, bordering Colombia) is an area of special interest because of its richness and the endemic character of some species. The high interchange of fishes is evident among the rivers with shared alluvial floodplains, and this has permitted a constant dispersal and colonization among the rivers of the Maracaibo Basin. Most of the species recorded from the floodplains south of the lake (e.g., *Apteronotus cuchillejo*, *Pterygoplichthys zuliaensis*, *Perrunichthys perruno*, *Platysilurus malarmo*) are associated with complex habitats of floodplains and backwater lagoons. The proportion of endemic species characteristic of the lowland floodplains reaches 70%, and only a few endemic species are restricted to high altitudes (e.g., *Astroblepus*). The province contains a very high proportion of primary freshwater species (75%). The richness diminishes toward the northeast, and in the Falcón coast even further east, nearly 40% of the primary floodplain species disappear. The coastal drainages of Falcón are depauperate faunas with a mixture of species from the Magdalena and Caribbean NSA domains, and around 50% are secondary species. The distribution records of the ichthyofauna and the current and past climatic conditions suggest that the arid drainages of eastern Maracaibo province have been colonized by species from rivers draining directly into the lake. These rivers, in a region of such high aridity and with intermittent flows, would not normally maintain such high species richness. In the early Pliocene, the time of the last glacial maximum (21–18 Ka) the greatest marine regression of recent times occurred, about 125 m below current sea level. At that time the Maracaibo basin would have had an even drier climate, but would probably have had more humid regions at the confluence of the Perijá and Andes mountains in the far south. Furthermore, given the shallow nature of the Gulf of Venezuela, the emergent lowlands would have created a large territory that would have permitted the dispersal of many species among drainages that today form separate units that make up the province (Galvis et al. 1997).

WESTERN, CENTRAL, AND EASTERN CARIBBEAN PROVINCES (CARIBBEAN NORTHERN SOUTH AMERICA DOMAIN)

The eastern limit of the Magdalena domain is evident (c. 5 % similarity) in the drainages of the arid Falcón coast (Figure 15.1) where a radical replacement of taxa that make up the ichthyofauna is evident. Two areas of endemism are evident, the Aroa-Yaracuy and Tuy drainages, which together contribute the major percentage of the species richness and endemism of the province. Rodríguez-Olarte and colleagues (2009) recognized three provinces (Western, Central, and Eastern Caribbean) within this domain, divided into several subprovinces. The Western Caribbean province has the greatest species richness (72 spp.) as well as endemism (23 spp.; 32%).

The Tocuyo drainage, with its origin in the northern Andean flanks, is lacking certain groups, such as the family Astroblepidae, that are common on the other (southern) side of the Andes and also occur in the Maracaibo Basin (Maldonado-Campo et al. 2005). This hiatus in the distribution of some families is apparently related to geographic barriers, climatic conditions, and extinction. In the Aroa and Yaracuy drainages we found species from other provinces and even species from the Orinoco Basin (Rodríguez-Olarte et al. 2006). Just how such a small area can contain so many species, high endemism and species from the Orinoco Basin is explained

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by the area's geographical isolation, the capture of rivers from adjacent drainages and the existence of hydrographic refuges in the foothills of mountain slopes. The Yaracuy depression occurs inside a drainage formed during the Tertiary or Quaternary by the Boconó and Morón faults (Schubert 1983). This drainage has been significantly isolated since the Pliocene, and has been affected by regional mountain building and changes in sea level. Such isolation fomented a rapid process of vicariant speciation, expressed in several lineages (Characidae, Loricariidae, etc.). There was probably interchange among the Orinoco and Caribbean drainages in the area of the upper Yaracuy river watershed uplifting, because the current data demonstrate that these drainages contain species of Orinoco origin (Rodríguez-Olarte et al. 2006). This would contribute to an elevation of the number of species present in these drainages, and it agrees with the hydrogeologic hypothesis, regarding the changes in the richness and distribution of species not explained by contiguous drainages (Hubert and Renno 2006).

In the Central Caribbean province, the ichthyofauna in the Unare drainage is quite similar to that of the Orinoco. The low-altitude separation of this coastal drainage from the Orinoco, as well as the deposition of sediments from Orinoco River in the eastern floodplains of the Unare, suggests a past connection. The final changes in the paleodrainage of the proto-Orinoco may have incorporated the Unare River as an aquatic corridor (freshwater and/or marine) between the Orinoco River and the Caribbean Sea. The Lake Valencia drainage shares species with neighboring drainages, including the Orinoco Basin. It is generally given that the separation of the drainage of Lake Valencia from that of the Tuy occurred in the Pleistocene (López-Rojas and Bonilla-Rivero 2000) and that recent tectonic events in the Interior mountain range indicate that this connection in the Victoria and Tácata faults occurred in the Quaternary. Currently, some species are recognized as endemic to the Valencia drainage (e.g., *Atherinella venezuelae*, *Lithogenes valencia*, *Pimelodella tapatapae*). But others, once thought endemic, such as *Moenkhausia pittieri*, have also been found in the Tuy drainage, indicating a past connection. The low species diversity in this endorheic drainage can be explained by climatic instability: according to Leyden (1985) and Curtis and colleagues (1999), in the Pleistocene this lake was surrounded by an area of extreme aridity, a phenomenon that was repeated and extensive at other times in its history. Between 13 and 12 Ka the local climate was semiarid, and the lake had ephemeral conditions, but around 10 Ka the lake was shallow and endorheic and had saline conditions (Bradbury et al. 1981); nevertheless, around 9 Ka the lake was recognized as freshwater. The extreme and repeated climatic changes in the Valencia drainage reduced the ichthyofauna drastically, with only remnants surviving in some tributaries of the highlands. The ancient saline conditions indicated for part of the history of Lake Valencia would explain the presence of an endemic pelagic species (*Atherinella venezuelae,* today endangered with extinction), a genus that generally occurs in estuaries (Unger and Lewis 1991). The lake flowed into the Cojedes River (Orinoco Basin), but this outlet was not constant, being evident around 8–3 Ka as a result of the overflow of the lake toward the western plains (Leyden 1985; Curtis et al. 1999). This could have served as a corridor for the exchange of fish species between the Orinoco and the Aroa and Yaracuy drainages, since currently the Turbio River runs into the Cojedes River.

In the Eastern Caribbean province, the Neverí, Manzanares, and Cariaco rivers have the lowest richness of the domain.

Even though *Serrasalmus neveriensis* is reported as endemic from the Neverí River, very few other records of endemics are truly from this drainage, and correspond instead to the Tuy River. In some drainages of the Eastern Caribbean, species occur, including a few endemics (*e.g., Bryconamericus lassorum*) that are not reported from other Caribbean slopes. Most of the species in this province are associated with the Orinoco faunas, indicating a lower similarity with the drainages to the Caribbean domain. The San Juan Atlantic drainage contains principally an Atlantic biota. The island of Trinidad, to the contrary of what we might expect given its climate and degree of isolation, has neither high species richness nor high endemism. These lacks may be due to changes in sea level and multiple recolonizations from the mainland, which would have affected the lowland areas of the island and might explain the high genetic diversity observed in some groups (e.g., Cyprinodontidae; Jowers et al. 2007). Today, the separation between the continent and Trinidad is very small, and the shallow depths that exist between them indicate that during lower sea levels (c. 20 ka) the island would have been joined to the continent by lowlands drained by rivers that could have united the island and the continent into one common drainage, thus permitting the interchange and dispersal of freshwater fishes. Even during times of higher sea levels later on, the freshwater plume of the Orinoco and other local rivers would have decreased the salinity greatly. Even today, the Gulf of Paria can experience fluctuations from the normal dry season values of 30‰ down to 5‰ at the peak of the rainy season and maximum Orinoco discharge (Kenny 1995). This observation explains why the Trinidadian fish fauna shares 60% of its species with the continental drainages of the Gulf of Paria. Previous analyses of species richness suggest that the dispersal and recent colonization by part of the continental fish fauna into other coastal drainages would have a localized affect, principally in the Gulf of Paria, the island of Trinidad, and the coasts and islands to the north of the Araya and Paria peninsulas. Even though the Orinoco Delta has been and continues to be a constant nucleus of dispersal for fishes along the coast of NSA, the intensity of its effect is variable, and the dilution of freshwaters, together with changes in the depth of the continental platform along the ocean coast, limits the dispersal of freshwater fishes in this region (Rodríguez-Olarte et al. 2009).

EVOLUTION OF ICHTHYOFAUNAS IN MAGDALENA AND MARACAIBO DRAINAGES

The principal events that have molded the modern fish fauna of the Magdalena and Maracaibo basins, as well as all of NSA, have been considered from many different points of view (Eigenmann 1905, 1920, 1922, 1923; Schultz 1949; Mago-Leccia 1970; Pérez and Taphorn 1993; Galvis et al. 1997; Lundberg et al. 1998; Lundberg and Aguilera 2003; Albert et al. 2006; Lovejoy et al. 2006; Rodríguez-Olarte et al. 2009). We maintain, as have many others, that there is no unique origin for the fish faunas of NSA. Our main limitation for unraveling these origins and the construction of biogeographic units is the current state of species-level taxonomy. The analyses of distribution we applied indicate that this is clearly the case for the Magdalena and Maracaibo basins, where the geologic history is a strong explicative component, but we believe that variation in climate in recent times has molded the evolution of modern fish faunas in NSA. Here we present a condensed sequence of the main events.

1. Paleodrainages—Around 50 million years ago extensive marine incursions covered the lowland areas of NSA, in what is today known as the llanos of Colombia and Venezuela. From the Early to Late Oligocene (c. 34–23 Ma) the great continental proto-Orinoco-Amazon river drained parts of the Guiana and Brazilian shields, and collected waters from the central and northern Andes while its eastern flanks were in contact with marine environments. From the Early to Late Miocene (c. 23–9 Ma), a great hydrosystem known as Lake Pebas is thought to have collected the waters of the central Amazon drainages, but on its northern edge (the extreme south of NSA) it would still have bordered the sea. In NSA the eastern flank of the Andes would have started to enter into contact with the continental drainages to the south, whether because of marine regression or as a result of changes in river drainage patterns. It may be assumed that the ancestral fish fauna was both highly diverse and widely distributed (Albert et al. 2006; see Chapter 7).

2. First Great Change: The Pacific Vicariance—An important body of evidence indicates that during the Middle Miocene (c. 15–10 Ma) the central-western regions and northern portions of the South American continent drained into a delta region that was located in what is today the Lake Maracaibo Basin, the same drainage pattern that existed since the Paleocene. The subduction of the Caribbean plate underneath the South American plate produced the uplifting of the central Cordillera of Colombia and the separation of the fish faunas of NSA from those of the Pacific (Atrato, Baudó; Duque-Caro 1990a), while volcanic islands began to appear in the region now occupied by the Isthmus of Panama. A widespread extensive lowland fish fauna was in place before this vicariant event. The last great and extensive marine incursion event in NSA is dated at around 15–10 Ma, during which time it is estimated that seas rose some 150 m or more (Haq et al. 1987), although Miller and colleagues (2006) suggest less extreme levels of 30–50 m (see Chapter 6). Regardless of the exact level of the rise, marine transgressions would have caused the retraction and partial extinction of the lowland fish faunas in many parts of NSA, and may have also provided a route for the introduction of marine-derived clades into the freshwater faunas of NSA (Lovejoy et al. 2006; see Chapter 17). The subsequent ascent of the Andes would permit further evolution of species, such as the separation of *Potamotrygon magdalenae* and *P. yepezi* in the Magdalena and Maracaibo basins, respectively. Stratigraphic evidence indicates that the ancestral fish fauna of NSA was highly diverse. Fossil records of fishes (*Arapaima*, *Brachyplatystoma*, *Plagioscion*, *Lepidosiren*, *Phractocephalus*, *Colossoma*) and other vertebrate faunas associated with large river systems, such as giant freshwater turtles (*Chelus*) that were found in Colombia in the Magdalena drainage and the Falcón coast in Venezuela (Urumaco) but that are now extinct in those regions, indicate that the ancestral distribution was widespread for these fishes (Lundberg 1998; Lundberg and Aguilera 2003; Dahdul 2004) and included Caribbean slopes (see Chapter 6).

3. Second Great Change: The Caribbean Vicariance—The initiation of the rise of the Eastern Cordillera of Colombia (c. 12 Ma, late Middle Miocene) caused one of the great divisions of fish faunas in NSA. At around 13 Ma (Early Miocene) meanders and braided chains predominated in the Magdalena valley, but headwaters originated far off in the western Guiana Shield (Hoorn et al. 1995). Then at about 12 Ma the Eastern Cordillera began to rise, which would separate the Magdalena drainage from the Orinoco. The definitive event separating the

Magdalena and Maracaibo basins was the ascent of the Mérida Andes and the Perijá Chain (c. 8 Ma; Late Miocene), which would also cut Maracaibo off from the Orinoco. The Orinoco then had to change course to the east, eventually emptying into the Caribbean through the modern Unare river drainage (Díaz de Gamero 1996). The Amazon would assume its modern configuration later at around 10 Ma, when Lake Pebas found an outlet to the east (Dobson et al. 2001), separated from the Orinoco, and began to drain into the Atlantic at Isla de Marajo.

The joining of the Perijá range with the Mérida Andes strongly affected the Magdalena and Maracaibo biotas. The Magdalena drainage no longer received the tremendous rainfalls from the trade winds, which now deposited their waters on the eastern slopes of the Perijá in the Maracaibo basin. In addition to being a vicariant event, the rise of the Mérida Andes contributed to the aridification of the Magdalena, probably contributing to the extinction of the many members of the freshwater biota that had flourished there for millions of years (Galvis et al. 1997). In the modern Magdalena drainage, as in many drainages throughout NSA, the majority of fish species are of small body size (58% with <100 mm TL). This is possibly due to the combined effects of climatic perturbations that reduced optimum habitats for larger species. As stated earlier, the increased aridity of the Magdalena drainage drastically reduced the discharge of its rivers and, concomitantly, the size of its floodplains. However, the southern and eastern portions of the Maracaibo Basin became very humid.

4. Marine Transgressions and Extinctions—The ascent of the Mérida Andes also contributed to the geological stability of the Maracaibo microplate, causing a deformation and/or inclination that may have permitted the ingression of marine water into the basin (Albert et al. 2006). The dramatic rises in sea level documented in the Maracaibo Basin of up to 100 m, lasting from 5 Ma to 800 Ka (Nores 2004), certainly left a strong mark on the freshwater biota, and may have resulted in the loss of the majority of its primary and secondary freshwater fishes. This marine incursion, although small in areal extent, resulted in the almost complete destruction of the freshwater ecosystems of the floodplains, with only the piedmont and mountain regions retaining freshwater habitats. This regional rise in sea level would also presumably affect the Magdalena Basin, but given its much larger area the effects would have been less pronounced.

During such extensive marine incursions a significant portion of the fish fauna would have become extinct, because of the retraction of freshwater systems and the associated loss of freshwater habitats. These would have been replaced by estuarine systems, perhaps mangroves and sea-grass beds. Large migratory fluvial species (e.g., *Phractocephalus*, *Colossoma*, etc.) would probably be the first to die out. Several migratory species persist today in the Magdalena and Maracaibo basins, but few are of great size (e.g., *Pseudoplatystoma*, *Mylossoma*, *Platysilurus*, *Sorubim*, *Salminus*); this finding may reflect a differential effect of the reduction in river length required by larger migratory species. Following a partial extinction of the freshwater biota of the Maracaibo Basin, Albert and colleagues (2006) proposed a hybrid origin for the current fish fauna found there. The ascent of the Isthmus of Panama (c. 3 Ma) would be the definitive continental closure, favoring even more the dispersal and colonization of Lower Mesoamerica by fishes from NSA (S. Smith and Bermingham 2005). The changes in the marine currents off the Pacific coast may have also played a role in

dispersal of fishes along that coast, and the same may have occurred along the Caribbean slopes of the isthmus.

The high number of genera and species shared between the Magdalena and Maracaibo basins indicates the ancient connection between them. One plausible hypothesis suggests that the Magdalena River, or one of its branches, flowed between the Perijá Mountains and the Sierra Nevada of Santa Marta (today the drainages of the Cesar and Rancheria rivers), given the relatively low altitude of their floodplains (Pérez and Taphorn 1993). This hypothetical outlet of the Magdalena River, very near the Gulf of Venezuela, would have passed through the Oca Fault, the geological depression that has formed at the edges in contact between the tectonic plates of this region. This course would have permitted the mixing of the fish faunas, and might explain the presence of *Ichthyoelephas* (Prochilodontidae) in the Rancheria drainage, of *Brycon* in the upper Río Limón, and of *Rachovia brevis* in the lowlands of that same river.

In the more recent geological past, about 120,000 years ago, sea levels continued to fluctuate, perhaps reaching +9 m (Hearty et al. 2007). Such a rise would inundate most of the Maracaibo and Magdalena floodplains, but because of the differences in geography, the effects in Maracaibo were much more drastic and would have left only the piedmont and mountains free of marine influence. In the Orinoco Andean piedmont, several species, such as *Brycon whitei*, *Colossoma macropomum,* and *Salminus hilarii*, reproduce in a small transition zone between the piedmont and high llanos (Rodríguez-Olarte and Kossowski 2004); similar areas would have survived in the Magdalena drainage but would have been lost in the Maracaibo. The elevation of sea level would cause the retraction of freshwater habitats and the extirpation or division into allopatric populations of many freshwater species, but might favor speciation of mountain species that would no longer be in contact. This might explain the high levels of endemic loricariids in the Maracaibo Basin highlands. These fishes, which are often associated with torrential mountain streams and piedmont rivers, may have experienced isolation into many different populations and lower levels of competition where migratory competitors had been eliminated.

In contrast, only 20–18 Ka it is estimated that sea levels dropped by as much as 120 m below current levels; while in the Holocene (c. 8 Ka) it supposedly dropped about 15 m along the Venezuelan coasts (Rull 1999). This lower sea level would have allowed the confluence of many adjacent drainages in a new lower configuration of the valley and thus favored dispersal and colonization of freshwater fishes between drainages. Lake Maracaibo today has a maximum depth of about 35 m, and so it would have been completely exposed during maximum sea-level drops. During such time the Catatumbo River would have formed a channel to the Gulf of Venezuela, similar to the situation of the Orinoco in the Paria Gulf. In the Lake Maracaibo basin, this would favor the dispersal of species among different drainages, which explains the provinces that we have detected in this study. Some marine coasts, because

of their abrupt drop to great depths, do not permit the interconnection of adjacent river channels, even at low sea-level stands. Such is the case for the marine coasts of the Magdalena River and those of the Guajira Peninsula.

According to our classical understanding of species-area relationships (MacArthur and Wilson 1967), reduction in size of a watershed explains the consequent reduction of the number of fish species that can live there. As rivers shrink during drought, the quality and quantity of fluvial aquatic habitats is reduced, and lentic systems would become shallower and then disappear. The difficulty for dispersal imposed by arid conditions is evident today in the distribution patterns of freshwater fishes along the Venezuelan coast.

High precipitation predicts more fish species in a given area, as we report here for some of the more humid drainages. Humid drainages might have acted as refugia (hydrogeographic or Pleistocene refugia) during times of global aridity. Such areas would maintain sufficiently favorable conditions to permit the survival and even the speciation of freshwater fishes in the affected region. Once favorable conditions return, the fishes surviving in such refugia would then be able to disperse into adjacent regions. It has also been suggested that southern Maracaibo acted as a refuge for freshwater fishes (the "refugio paleoecológico Catatumbo" of Pérez and Taphorn 1993) and for some of the small, humid coastal drainages (Aroa and Tuy rivers) associated with the Coastal mountains (Rodríguez-Olarte et al. 2009). Usually, these watersheds have relatively high annual precipitation, intact widespread forest cover, and high endemism. The existence of a refuge in southern Maracaibo might help to explain the relatively high species richness observed there today in light of the drastic impacts of drier climate and changes in sea levels. In the rest of the drainages of NSA, a few other possible refugia can be detected, such as the Atrato of northern Colombia, where precipitation is among the highest recorded for the world and produces the highest discharge of water for all rivers of NSA, 4,500 m^3/s. A similar situation exists in the watersheds of the nearby Darién region of Panama. The presence of a hydrographic refuge in this region has great relevance to the dispersal of and colonization by freshwater fishes of Lower Central America.

ACKNOWLEDGMENTS

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