



# The biogeography of lower Mesoamerican freshwater fishes

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## ABSTRACT

**Aim** This paper examines the importance of regional processes in determining the patterns of distribution and diversity of lower Mesoamerican freshwater fishes.

**Location** We focused our analyses on the lower Mesoamerican region, which we define to include all the rivers of Panama and Costa Rica. The geographic boundaries are the Colombian Choco to the south and Lake Nicaragua to the north.

**Methods** We described the biogeographical provinces of lower Mesoamerica (LMA) using presence/absence data of primary and secondary LMA freshwater fishes. We conducted subsequent analyses at the spatial resolution of the biogeographical provinces and described patterns of community composition, species richness, endemism, range size, and the permeability of dispersal barriers between biogeographical provinces.

**Results** This study represents the first attempt since that of W. A. Bussing in 1976 to investigate the biogeographical regions of Mesoamerica, and our analyses demonstrate increased regional complexity in biodiversity patterns relative to previous studies. Changes in community composition across LMA clearly highlight the importance of both extrinsic geological processes and intrinsic biological differences among freshwater fish species in shaping the dispersal and diversification histories of the LMA freshwater fish fauna. The influence of biology and geology is also exemplified by patterns of endemism and turnover between biogeographical provinces, which suggests that the relative importance of regional speciation and dispersal varies spatially across the LMA landscape. Finally, it would seem to follow that secondary freshwater fishes will have larger range sizes than primary fishes as a result of the increased salinity tolerance posited for the former group, and thus the increased probability of dispersal along coastlines. We did not, however, find a significant difference between the average range size of primary and secondary freshwater fishes, indicating that the putative differences in physiological tolerance to seawater between the two groups are not reflected in their distribution patterns at the scale of LMA. The geometric distribution of range size of LMA freshwater fishes suggests that dispersal of both primary and secondary freshwater fishes along coastlines must be infrequent.

**Main conclusion** The observation that regional processes exerted a strong influence on the assembly and maintenance of LMA freshwater fish communities has important consequences for both theory and conservation. We suggest that large-scale biogeographical analyses are required to illuminate the backdrop upon which local interactions play themselves out, supporting a top-down approach to the study of biological diversity. Our results also identify areas of high conservation priority, providing a baseline for informing conservation strategies for freshwater fishes in LMA. We conclude by calling for conservation planning and action that acknowledges the importance that regional processes play in

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determining patterns of organismal diversity, and that incorporates these processes in strategies to conserve remnant biological diversity.

### Keywords

Beta diversity, biogeography, community assembly, dispersal, freshwater fish, Mesoamerica, regional processes, species richness.

## INTRODUCTION

Identification of the relative contributions of local and regional processes in determining patterns of species richness is essential to understanding the mechanisms underlying patterns of global species richness (Huston, 1999; Gaston, 2000). Traditionally, ecologists have focused on the importance of local, deterministic processes such as competition, predation and mutualism in shaping patterns of species richness and community composition (Ricklefs, 1987). More recently, ecologists have emphasized the role that regional processes, such as dispersal, speciation and extinction, play in the assembly and maintenance of biological communities (Ricklefs, 1987, 2004; Ricklefs & Schluter, 1993; Gaston, 2000, 2003; Mora *et al.*, 2003; Smith *et al.*, 2004; Smith & Shurin, in press). However, it has seldom been possible to directly evaluate the importance of regional processes in determining patterns of distribution and diversity for entire continental faunas because molecular phylogeographic analyses have only recently begun to illuminate historical patterns of colonization and community assembly (Bermingham & Avise, 1986; Losos, 1992; Qian & Ricklefs, 1999, 2000; Losos & Schluter, 2000; Parra-Olea & Wake, 2001; Ricklefs & Bermingham 2001; Mueller *et al.*, 2004), and reliable presence/absence data at the continental scale remain scarce for most taxa found in tropical and subtropical regions of the world (but see Unmack, 2001).

Lower Mesoamerica (LMA) provides an interesting backdrop against which to study the importance of regional processes. The Pliocene completion of the Isthmus of Panama connected North and South America, permitting a massive exchange of flora and fauna between the two continents, an event termed the Great American Biotic Interchange (Marshall *et al.*, 1979; Stehli & Webb, 1985). The emerging isthmus enabled the initial colonization of Mesoamerica by freshwater fishes from putative source populations in north-western Colombia (Miller, 1966; Myers, 1966; Bussing, 1985; Bermingham & Martin, 1998). However, the embryonic isthmus provided differential colonization opportunities for these fishes (Miller, 1966; Myers, 1966; Bussing, 1976, 1985; Bermingham & Martin, 1998; Martin & Bermingham, 1998; Perdices *et al.*, 2002). Secondary freshwater fishes such as cichlids and *Rivulus* colonized Mesoamerica between 18 and 15 Ma (Martin & Bermingham, 1998; see also Murphy & Collier, 1996), approximately 10 Ma earlier than did primary freshwater fishes (Bermingham & Martin, 1998), according to molecular clock estimates.

Two important facts suggest that the study of patterns of distribution and diversity of LMA freshwater fishes will permit inferences regarding the role that regional processes played in the assembly and maintenance of freshwater fish communities in

this region. First, although there has been controversy regarding the timing of the arrival of primary freshwater fishes in Mesoamerica (Miller, 1966; Myers, 1966; Bussing, 1985), molecular systematic research indicates that the evolutionary assembly of the LMA freshwater fish fauna is recent (Bermingham & Martin, 1998; Perdices *et al.*, 2002), suggesting that the historical record of colonization is largely intact because it is not likely to have been overwritten by multiple rounds of dispersal. Second, drainage basins function as terrestrial islands that create repeated patterns of subdivision of populations and communities within discrete boundaries. These patterns arise largely because of the dispersal constraints on obligate (primary and secondary) freshwater fishes. Primary freshwater fishes are hypothesized to be physiologically intolerant of saline conditions and thus rarely cross marine barriers (Myers, 1938, 1966; Unmack, 2001). The dispersal of primary freshwater fishes is thought to be entirely dependent on the formation of direct connections between drainage basins arising from physiographical changes of the landscape. Examples include river anastomosis that occurs during periods of reduced sea level coinciding with glacial maxima, as well as during the high water of the rainy season, pulses of freshwater that connect rivers along the coast during flood events, and river capture events that result from differential erosion across drainage divides (Myers, 1938, 1966; Loftin, 1965; Miller, 1966; Bermingham & Martin, 1998; Unmack, 2001). On the other hand, secondary freshwater fishes are hypothesized to tolerate moderate levels of salinity and thus may be able to disperse via saline marine waters along coastlines, although the frequency of such colonization events remains unknown. Recent colonization of LMA by obligate freshwater fishes coupled with the dispersal limitation of these fishes therefore provides an interesting system in which to study the importance of regional processes in determining present-day patterns of distribution and diversity.

A first step towards studying the importance of regional processes is the description of biogeographical provinces. Biogeographical provinces represent geographical regions of relatively homogeneous faunal composition, and their description permits analysis of the processes responsible for turnover across the landscape, in terms of both species richness and community composition. We describe the biogeographical provinces of LMA freshwater fishes and test whether the biogeographical provinces represent areas of shared history that extend beyond the similarity arising simply from the spatial arrangement of the rivers and the source of colonists. In turn, we evaluate patterns of community composition, species richness and endemism at the scale of biogeographical provinces in order to document physiological and regional influences on the

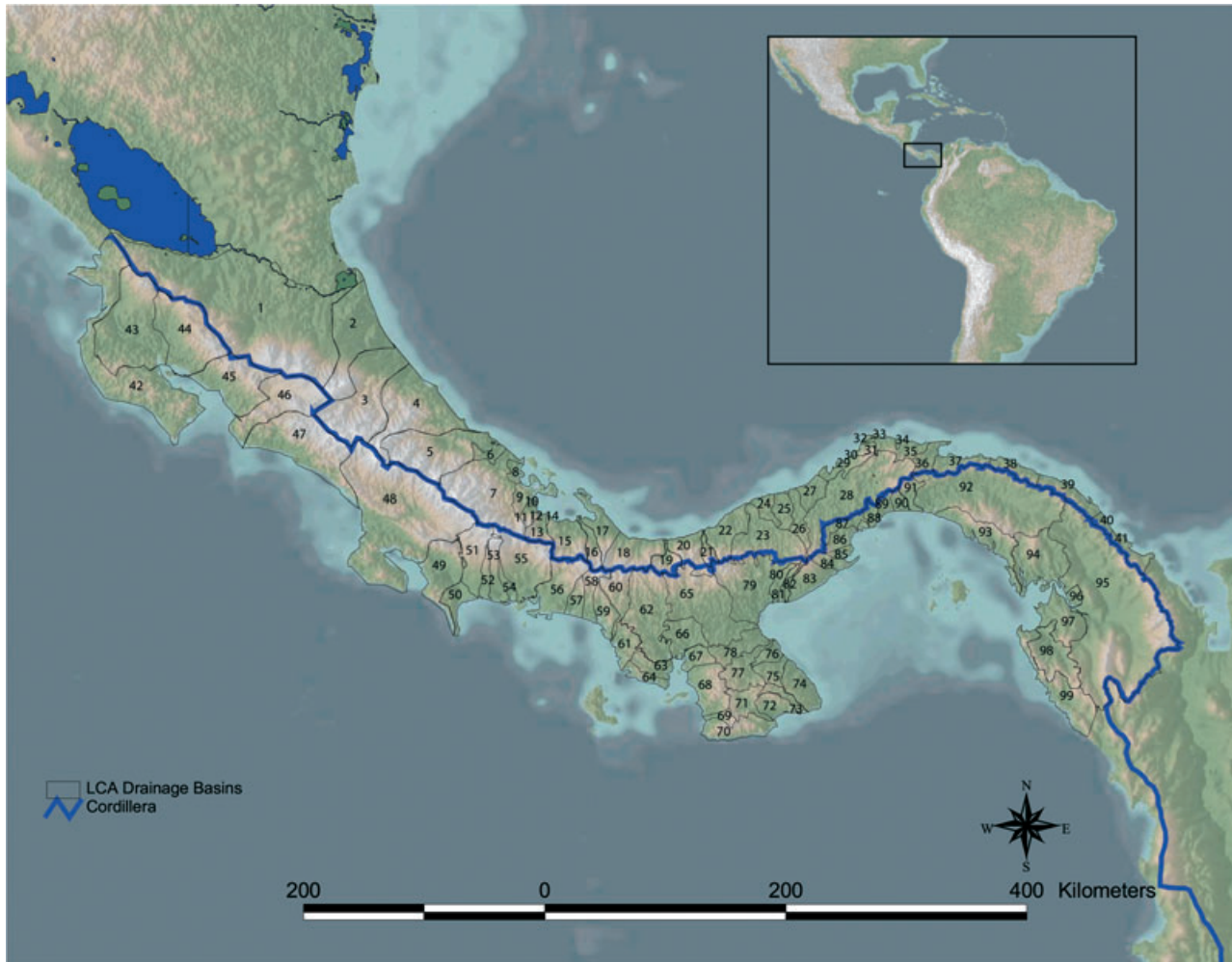
dispersal and diversification history of the Mesoamerican freshwater fish fauna. Furthermore, we quantify the biological turnover between biogeographical provinces in order to estimate how the relative permeability of geographical barriers to dispersal changes across the LMA landscape. Finally, we assess the range-size distribution of the LMA freshwater fishes by determining the number of biogeographical provinces occupied by each species, and we test whether hypothesized differences in salinity tolerance between primary and secondary freshwater

fishes have influenced the sizes of the geographical ranges of these fishes.

## METHODS

### Data sources

We assembled a data base describing the presence and absence of freshwater fish species in LMA drainage basins, a region



**Figure 1** Drainage basins of lower Mesoamerica. 1, Rio San Juan; 2, Rio Tortuguero; 3, Rio Parismina; 4, Rio Matina; 5, Rio Sixaola; 6, Rio San San; 7, Rio Changuinola; 8, International Cuenca no. 91; 9, Rio Uyama; 10, Quebrada Cilico Creek and Quebrada Marin; 11, Rio Robalo; 12, Quebrada La Gloria; 13, Rio Guarumo; 14, Quebrada La Margarita; 15, Rio Guariviara; 16, Rio Cricamola; 17, Rio Canaveral; 18, International Cuenca no. 95; 19, Rio Calovebora; 20, International Cuenca no. 99; 21, Rio Veraguas; 22, International Cuenca no. 103; 23, Rio Cocle del Norte; 24, International Cuenca no. 107; 25, Rio Miguel de la Borda; 26, Rio Indio; 27, International Cuenca no. 113; 28, Rio Chagres; 29, Rio Piedras; 30, Rio Cuanche; 31, Rio Cascajal; 32, Rio Claro; 33, Rio Pina Pina; 34, Rio Frio; 35, Rio Cuango; 36, Rio Mandinga; 37, International Cuenca no. 121; 38, Rio Azucar; 39, Rio Playon Chico; 40, Rio Cuadi; 41, Rio Acla; 42, Rios of the Nicoya Peninsula; 43, Rio Tempisque; 44, Rio Bebedero; 45, Rio Barranca; 46, Rio Tarcoles; 47, Rio Pirris; 48, Rio Terraba; 49, Rio Coto; 50, Rio Palo Blanco; 51, Rio Chiriqui Viejo; 52, Rio Escarrea; 53, Rio Chico; 54, Rio Platanal; 55, Rio Chiriqui; 56, Rio Estero Salado; 57, Rio San Juan; 58, Rio San Felix; 59, Rio Santiago; 60, Rio Tabasara; 61, Rio Bubi; 62, Rio San Pablo; 63, Rio Cate; 64, Quebrada Seca; 65, Rio Santa Maria; 66, Rio San Pedro; 67, Rio Ponuga; 68, Rio Tebario; 69, Rio Pavo; 70, Rio Playita; 71, Rio Tonosi; 72, Rio Cana; 73, Rio Oria; 74, International Cuenca no. 126; 75, Rio Guarare; 76, Rio Honda; 77, Rio La Villa; 78, Rio Parita; 79, Rio Cocle del Sur; 80, Rio Chorrera; 81, Rio Estancia; 82, Rio Anton; 83, Rio Farallon; 84, Rio Chame; 85, Rio Sajalices; 86, Rio Capira; 87, Rio Caimito; 88, Rio Grande; 89, Rio Juan Diaz; 90, Rio Cabra; 91, Rio Pacora; 92, Rio Bayano; 93, International Cuenca no. 150; 94, Rio Lara; 95, Rio Tuira; 96, Rio Iglesia; 97, International Cuenca no. 160; 98, Rio Samba; 99, International Cuenca no. 164.

including the rivers of Panama and Costa Rica (Fig. 1). Our data base was based on information of species distribution contained in the NEODAT data base (<http://www.neodat.org>) and the Smithsonian Tropical Research Institute (STRI) Freshwater Fish Collection (Bermingham *et al.*, 1997a). We geo-referenced and verified each record's merit using the literature and the STRI Freshwater Fish Collection. Only collection records for primary and secondary freshwater fishes were used in the analyses. No diadromous fishes were included in our analyses. A total of 18,366 records, representing the distribution of 170 species, 72 genera and 23 families, were included in our analyses.

### Assumptions

Given the heterogeneity in collecting effort across rivers, we documented many local absences of fish species that can be attributed to insufficient sampling effort exerted in particular drainages. The fairly dense sampling of rivers across the isthmian landscape, however, suggests that absence of a fish species at the provincial level can be assumed to be real. Since all of our analyses were undertaken at the provincial level, the inferences that we make were not unduly influenced by absences arising from insufficient sampling effort in some drainage basins.

There are also some limitations in the taxonomic description of the fauna. For example, recent molecular systematic research on the genus *Roebooides* (Bermingham & Martin, 1998) uncovered phylogenetic variation that made geographical sense of a bewildering distribution pattern based on the preceding taxonomy and that led to the description of three new species (Lucena, 2000). That said, we are confident that our description of both taxa and geographical distributions is largely correct because phylogenetic relationships of most potentially problematic taxa have been clarified by molecule-based phylogeographic analyses (Bermingham & Martin, 1998; Martin & Bermingham, 2000; Perdices *et al.*, 2002). Table 1 provides a complete list of the freshwater fish species of LMA as defined by prevailing taxonomy and molecular phylogeography, and their distribution in the LMA biogeographical provinces.

### Biogeographical provinces

Correspondence analysis was used to convert binary species presence/absence data into continuous variables (Jackson & Harvey, 1989; Huguéy & Leveque, 1994). This method of ordination positions the objects (sites and species) in a space that contains fewer dimensions than the original data set (Legendre & Legendre, 1998). It thus simplifies the recovery of meaningful patterns in the first ordination axes and defers noise to later axes (Gauch, 1982). The noise eliminated by the correspondence analysis is assumed to be non-informative from a biogeographical perspective (Huguéy & Leveque, 1994). Correspondence analysis is preferred over other methods of multivariate analysis because it is based on a metric that does not include cases in which two species are

both absent from a given locality in its computation (Huguéy & Leveque, 1994), and is thus strongly recommended for ecological or biogeographical multivariate analyses that rely on binomial data (Legendre & Legendre, 1998).

Next, Euclidian distances were used to compute the faunistic distances between the rivers based on the coordinates representing the first three axes of the correspondence analysis. An unweighted pair group method with arithmetic mean (UPGMA) analysis produced a dendrogram depicting the faunistic relationship between drainage basins for the LMA freshwater fish fauna.

The faunistic relationship between rivers was also described using Jaccard's similarity coefficient, a method that did not involve the use of correspondence analysis to transform the data initially. The UPGMA cluster analysis produced a dendrogram describing the faunistic relationship between drainage basins based on Jaccard's similarity coefficient (the procedures described in the preceding paragraphs of this section were implemented in MVSP v3.1, Provalis Research, Montreal, Quebec).

We transformed the values of the UPGMA cluster matrices (for clusters based on both Euclidean distances and Jaccard's similarity coefficient) to matrices of cophenetic (ultrametric) distances. We then subjectively tested the goodness-of-fit of our UPGMA clusters by calculating a cophenetic correlation based on the cophenetic distance matrix and the original distance matrix (Euclidean or Jaccard) that was used in the UPGMA analysis. The cophenetic correlation measures the extent to which the clustering results correspond to the original resemblance matrix (Legendre & Legendre, 1998). A cophenetic correlation coefficient of  $> 0.9$  represents a very good fit, whereas a coefficient of  $0.8 < r < 0.9$  represents a good fit to the data (these analyses were performed in NTSYSpc2.1, Exeter Software, New York, USA).

In addition, two partial Mantel tests were performed to test the significance of the faunistic relationships among drainage basins described by Euclidean distances and Jaccard's similarity coefficient (R Package v4.0). The data were first partitioned into two randomly defined groups of species ( $y$  and  $z$ ). We used Euclidean distances (or Jaccard's similarity coefficient) to produce two matrices that described the faunistic similarity between the rivers for species group  $y$  and species group  $z$  ( $x(y)$  and  $x(z)$ ). The Nearest Features extension of Arcview GIS (Jenness Enterprises, <http://www.jennessent.com>) was used to calculate the geographical distance between each pair of drainage basins, resulting in a third matrix, the geographical distance matrix. A partial Mantel test was then performed on the faunistic distance matrices, using the geographical distance matrix to remove the effect of the spatial positioning of the drainage basins, in order to determine if the faunistic relationships depicted in our dendrograms arose because of the spatial positioning of the drainage basins alone.

Finally, we described the biogeographical provinces of LMA by identifying convergent results between the UPGMA dendrograms. In cases for which the dendrograms based on

**Table 1** The LMA freshwater fish species by their occurrence in the described biogeographical provinces. We assembled a data base describing the presence and absence of freshwater fish species in LMA drainage basins, a region including the rivers of Panama and Costa Rica. The biogeographical provinces in this table refer to the areas of faunal similarity described by our analyses. The Salinity tolerance column refers to the hypothesized salinity tolerance of freshwater fishes based on Myers (1949)

Salinity tolerance	Family	Species	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
1	Ageneiosidae	<i>Ageneiosus caucanus</i>	0	0	0	0	0	0	1
1	Apteronotidae	<i>Apteronotus rostratus</i>	0	0	0	0	0	0	1
1	Astroblepidae	<i>Astroblepus longifilis</i>	0	0	0	0	0	1	1
1	Astroblepidae	<i>Astroblepus trifasciatum</i>	0	0	0	0	0	1	1
1	Auchenipteridae	<i>Parauchenipterus amblops</i>	0	0	0	0	1	0	1
1	Callichthyidae	<i>Hoplosternum punctatum</i>	0	0	0	0	0	1	1
1	Characidae	<i>Astyanax aeneus</i>	1	1	1	1	1	1	1
1	Characidae	<i>Astyanax nasutus</i>	1	0	0	0	0	0	0
1	Characidae	<i>Astyanax orthodus</i>	0	0	1	0	0	0	0
1	Characidae	<i>Astyanax panamensis</i>	0	0	0	0	0	1	1
1	Characidae	<i>Astyanax ruberrimus</i>	0	0	0	0	1	1	1
1	Characidae	<i>Bramocharax bransfordii</i>	1	0	0	0	0	0	0
1	Characidae	<i>Brycon argenteus</i>	0	0	0	0	0	1	1
1	Characidae	<i>Brycon behreae</i>	0	0	0	1	1	0	0
1	Characidae	<i>Brycon chagrensis</i>	0	0	0	0	0	1	0
1	Characidae	<i>Brycon guatemalensis</i>	1	0	1	0	0	0	0
1	Characidae	<i>Brycon obscurus</i>	0	0	0	0	1	1	0
1	Characidae	<i>Brycon petrosus</i>	0	0	0	0	0	1	1
1	Characidae	<i>Brycon</i> sp. nov. 'Acla'	0	0	0	0	0	1	0
1	Characidae	<i>Brycon</i> sp. nov. 'Bocas'	0	0	1	0	0	0	0
1	Characidae	<i>Brycon striatulus</i>	0	0	0	0	0	0	1
1	Characidae	<i>Bryconamericus emperador</i>	0	0	1	0	1	1	1
1	Characidae	<i>Bryconamericus ricae</i>	0	0	1	0	0	0	0
1	Characidae	<i>Bryconamericus scleroparius</i>	1	0	1	0	0	0	0
1	Characidae	<i>Bryconamericus terrabensis</i>	0	0	0	1	0	0	0
1	Characidae	<i>Bryconamericus zeteki</i>	0	0	0	0	1	0	0
1	Characidae	<i>Carlana eigenmanni</i>	1	0	0	0	0	1	0
1	Characidae	<i>Characidium marshi</i>	0	0	0	0	0	0	1
1	Characidae	<i>Compsura dialeptura</i>	0	0	0	1	1	0	0
1	Characidae	<i>Compsura gorgonae</i>	0	0	0	0	1	1	1
1	Characidae	<i>Compsura mitoptera</i>	0	0	0	0	0	1	0
1	Characidae	<i>Compsura</i> sp. nov. 'Chiriqui'	0	0	0	1	0	0	0
1	Characidae	<i>Creagrutus affinis</i>	0	0	0	0	0	0	1
1	Characidae	<i>Eretmobrycon bayano</i>	0	0	0	0	0	0	1
1	Characidae	<i>Gephyrocharax atricaudata</i>	0	0	0	0	0	1	1
1	Characidae	<i>Gephyrocharax chocoensis</i>	0	0	0	0	0	1	0
1	Characidae	<i>Gephyrocharax intermedius</i>	0	0	0	1	1	1	0
1	Characidae	<i>Gephyrocharax</i> sp. nov. 'Chiriqui'	0	0	0	1	0	0	0
1	Characidae	<i>Hemibrycon dariensis</i>	0	0	0	1	1	1	1
1	Characidae	<i>Hyphessobrycon panamensis</i>	0	0	1	0	0	1	0
1	Characidae	<i>Hyphessobrycon savagei</i>	0	0	0	1	0	0	0
1	Characidae	<i>Hyphessobrycon</i> sp. nov. 'Acla'	0	0	0	0	0	1	0
1	Characidae	<i>Hyphessobrycon</i> sp. nov. 'Bayano'	0	0	0	0	0	0	1
1	Characidae	<i>Hyphessobrycon</i> sp. nov. 'Bocas'	0	0	1	0	0	0	0
1	Characidae	<i>Hyphessobrycon tortugerae</i>	1	0	0	0	0	0	0
1	Characidae	<i>Phenagoniates macrolepis</i>	0	0	0	0	0	0	1
1	Characidae	<i>Pseudocheirodon affinis</i>	0	0	0	0	1	1	1
1	Characidae	<i>Pseudocheirodon terrabae</i>	0	0	0	1	0	0	0
1	Characidae	<i>Pterobrycon myrnae</i>	0	0	0	1	0	0	0
1	Characidae	<i>Roeboides bouchellei</i>	1	1	0	1	0	0	0
1	Characidae	<i>Roeboides carti</i>	0	0	0	0	0	1	0
1	Characidae	<i>Roeboides dayi</i>	0	0	0	0	0	1	0
1	Characidae	<i>Roeboides guatemalensis</i>	0	0	0	0	0	1	0

Table 1 continued

Salinity tolerance	Family	Species	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
1	Characidae	<i>Roeboides ilseae</i>	0	0	0	1	0	0	0
1	Characidae	<i>Roeboides occidentalis</i>	0	0	0	1	1	0	1
1	Characidae	<i>Roeboides</i> sp. nov. 'Cocle del Norte'	0	0	0	0	0	1	0
1	Ctenoluciidae	<i>Ctenolucius beani</i>	0	0	0	0	1	0	1
1	Curimatidae	<i>Cyphocharax magdalenae</i>	0	0	0	1	1	0	1
1	Erythrinidae	<i>Hoplias malabaricus</i>	0	0	0	0	0	1	1
1	Erythrinidae	<i>Hoplias microlepis</i>	0	0	0	1	1	1	1
1	Gasteropelecidae	<i>Gasteropelecus maculatus</i>	0	0	0	0	0	0	1
1	Gymnotidae	<i>Gymnotus cylindricus</i>	1	1	1	0	0	0	0
1	Gymnotidae	<i>Gymnotus maculosus</i>	1	1	0	0	0	0	1
1	Hemiodontidae	<i>Saccodon dariensis</i>	0	0	0	0	0	0	1
1	Lebiasinidae	<i>Piabucina boruca</i>	0	0	0	1	0	0	0
1	Lebiasinidae	<i>Piabucina festae</i>	0	0	0	0	0	0	1
1	Lebiasinidae	<i>Piabucina panamensis</i>	0	0	0	0	0	1	1
1	Loricariidae	<i>Ancistrus chagresi</i>	0	0	0	0	0	1	1
1	Loricariidae	<i>Ancistrus spinosus</i>	0	0	0	0	1	0	1
1	Loricariidae	<i>Chaetostoma fischeri</i>	0	0	0	0	0	1	1
1	Loricariidae	<i>Crossoloricaria variegata</i>	0	0	0	0	0	0	1
1	Loricariidae	<i>Dasylicaria capetensis</i>	0	0	0	0	0	0	1
1	Loricariidae	<i>Dasylicaria tuyrensis</i>	0	0	0	0	0	0	1
1	Loricariidae	<i>Hypostomus panamensis</i>	0	0	0	1	1	1	1
1	Loricariidae	<i>Lasiancistrus planiceps</i>	0	0	0	0	0	1	1
1	Loricariidae	<i>Leptoancistrus canensis</i>	0	0	0	0	1	1	1
1	Loricariidae	<i>Rineloricaria altipinnis</i>	0	0	0	0	0	0	1
1	Loricariidae	<i>Rineloricaria uracantha</i>	0	0	0	1	0	1	1
1	Loricariidae	<i>Sturisoma panamense</i>	0	0	0	0	1	0	1
1	Loricariidae	<i>Sturisomatichthys citurensis</i>	0	0	0	0	0	0	1
1	Pimelodidae	<i>Imparales panamensis</i>	0	0	0	0	1	1	1
1	Pimelodidae	<i>Nannorhamdia lineata</i>	0	0	0	1	0	0	0
1	Pimelodidae	<i>Pimelodella chagresi</i>	0	0	0	1	1	1	1
1	Pimelodidae	<i>Pimelodella</i> sp. nov. 'recent'	0	0	0	0	1	0	1
1	Pimelodidae	<i>Pimelodus clarias</i>	0	0	0	0	0	0	1
1	Pimelodidae	<i>Pseudopimelodus zungaro</i>	0	0	0	0	0	0	1
1	Pimelodidae	<i>Rhamdia laticauda</i>	1	1	1	1	1	1	0
1	Pimelodidae	<i>Rhamdia nicaraguensis</i>	1	1	0	0	0	0	0
1	Pimelodidae	<i>Rhamdia quelen</i>	1	1	1	1	1	1	1
1	Rhamphichthyidae	<i>Brachyhypopomus occidentalis</i>	0	0	1	1	1	1	1
1	Sternopygidae	<i>Eigenmannia humboldtii</i>	0	0	0	0	0	0	1
1	Sternopygidae	<i>Sternopygus macrurus</i>	0	0	0	1	1	0	1
1	Trichomycteridae	<i>Trichomycterus striatus</i>	0	0	0	1	1	1	1
2	Anablepidae	<i>Oxyzygonectes dovii</i>	1	1	0	1	1	0	0
2	Aplocheilidae	<i>Rivulus birkhahni</i>	0	0	1	0	0	0	0
2	Aplocheilidae	<i>Rivulus brunneus</i>	0	0	0	0	0	1	1
2	Aplocheilidae	<i>Rivulus chucunaque</i>	0	0	0	0	0	1	1
2	Aplocheilidae	<i>Rivulus frommi</i>	0	0	0	0	1	1	0
2	Aplocheilidae	<i>Rivulus fuscolineatus</i>	1	1	0	0	0	0	0
2	Aplocheilidae	<i>Rivulus hildebrandi</i>	0	0	0	1	1	0	0
2	Aplocheilidae	<i>Rivulus isthmensis</i>	1	1	1	0	0	0	0
2	Aplocheilidae	<i>Rivulus kuelpmanni</i>	0	0	1	0	0	0	0
2	Aplocheilidae	<i>Rivulus montium</i>	0	0	0	0	0	1	0
2	Aplocheilidae	<i>Rivulus rubripunctatus</i>	0	0	1	0	0	0	0
2	Aplocheilidae	<i>Rivulus</i> sp. nov. 'Rio Cocle del Norte'	0	0	0	0	0	1	0
2	Aplocheilidae	<i>Rivulus uroflammeus</i>	0	0	0	1	0	0	0
2	Aplocheilidae	<i>Rivulus wassamanni</i>	0	0	1	0	0	0	0
2	Aplocheilidae	<i>Rivulus weberi</i>	0	0	0	0	0	1	1
2	Cichlidae	<i>Aequidens coeruleopunctatus</i>	0	0	0	1	1	1	1

Table 1 continued

Salinity tolerance	Family	Species	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
2	Cichlidae	<i>Amphilophus calobrensis</i>	0	0	0	0	0	0	1
2	Cichlidae	<i>Amphilophus citrinellus</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Amphilophus lyonsi</i>	0	0	0	1	0	0	0
2	Cichlidae	<i>Amphilophus umbriferum</i>	0	0	0	0	0	0	1
2	Cichlidae	<i>Archocentrus centrarchus</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Archocentrus myrnae</i>	0	0	1	0	0	0	0
2	Cichlidae	<i>Archocentrus nanoluteus</i>	0	0	1	0	0	0	0
2	Cichlidae	<i>Archocentrus nigrofasciatus</i>	1	1	1	0	0	0	0
2	Cichlidae	<i>Archocentrus panamensis</i>	0	0	0	0	0	1	1
2	Cichlidae	<i>Archocentrus sajica</i>	0	0	0	1	0	0	0
2	Cichlidae	<i>Archocentrus septemfasciatus</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Astatheros alfari</i>	1	1	0	0	0	0	0
2	Cichlidae	<i>Astatheros altifrons</i>	0	0	0	1	0	0	0
2	Cichlidae	<i>Astatheros bussingi</i>	0	0	1	0	0	0	0
2	Cichlidae	<i>Astatheros calobrense</i>	0	0	0	0	0	0	1
2	Cichlidae	<i>Astatheros diquis</i>	0	0	0	1	0	0	0
2	Cichlidae	<i>Astatheros longimanus</i>	1	1	0	0	0	0	0
2	Cichlidae	<i>Astatheros rhytisma</i>	0	0	1	0	0	0	0
2	Cichlidae	<i>Astatheros rostratus</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Cichlasoma atromaculatus</i>	0	0	0	0	0	1	0
2	Cichlidae	<i>Geophagus crassilabris</i>	0	0	0	0	0	1	1
2	Cichlidae	<i>Herotilapia multispinosa</i>	1	1	0	0	0	0	0
2	Cichlidae	<i>Hypsophrys nicaraguensis</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Neetroplus nematopus</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Parachromis dovii</i>	1	1	0	0	0	0	0
2	Cichlidae	<i>Parachromis loisellei</i>	1	0	1	0	0	0	0
2	Cichlidae	<i>Parachromis managuensis</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Theraps sieboldii</i>	0	1	0	1	1	0	0
2	Cichlidae	<i>Theraps</i> sp. nov. 'Rio Viento'	0	0	1	0	0	0	0
2	Cichlidae	<i>Theraps underwoodi</i>	1	0	0	0	0	0	0
2	Cichlidae	<i>Vieja maculicauda</i>	1	0	0	0	0	1	0
2	Cichlidae	<i>Vieja tuyrensis</i>	0	0	0	0	0	0	1
2	Poeciliidae	<i>Alfaro cultratus</i>	1	1	1	0	0	0	0
2	Poeciliidae	<i>Belonesox belizanus</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Brachyrhaphis cascajalensis</i>	0	0	1	0	0	1	1
2	Poeciliidae	<i>Brachyrhaphis episcopi</i>	0	0	0	0	1	1	1
2	Poeciliidae	<i>Brachyrhaphis holdridgei</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Brachyrhaphis olomina</i>	1	1	0	0	0	0	0
2	Poeciliidae	<i>Brachyrhaphis parismina</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Brachyrhaphis rhabdophora</i>	1	1	0	1	0	0	0
2	Poeciliidae	<i>Brachyrhaphis roseni</i>	0	0	0	1	1	0	0
2	Poeciliidae	<i>Brachyrhaphis roswithae</i>	0	0	0	0	1	1	0
2	Poeciliidae	<i>Brachyrhaphis terrabensis</i>	0	0	0	1	0	0	0
2	Poeciliidae	<i>Gambusia nicaraguensis</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Neoheterandria cana</i>	0	0	0	0	0	0	1
2	Poeciliidae	<i>Neoheterandria tridentiger</i>	0	0	1	1	1	1	1
2	Poeciliidae	<i>Neoheterandria umbratilis</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Phallichthys amates</i>	1	1	1	0	0	0	0
2	Poeciliidae	<i>Phallichthys quadripunctatus</i>	0	0	1	0	0	0	0
2	Poeciliidae	<i>Phallichthys tico</i>	1	0	0	0	0	0	0
2	Poeciliidae	<i>Poecilia caucana</i>	0	0	0	0	0	0	1
2	Poeciliidae	<i>Poecilia gillii</i>	1	1	1	1	1	1	1
2	Poeciliidae	<i>Poeciliopsis elongata</i>	0	1	0	1	1	0	1
2	Poeciliidae	<i>Poeciliopsis paucimaculata</i>	0	0	0	1	0	0	0
2	Poeciliidae	<i>Poeciliopsis retropinna</i>	0	0	0	1	0	0	0
2	Poeciliidae	<i>Poeciliopsis</i> sp. nov. 'La Yeguada'	0	0	0	0	1	0	0

**Table 1** *continued*

Salinity tolerance	Family	Species	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
2	Poeciliidae	<i>Poeciliopsis turrubarensis</i>	0	1	0	1	1	0	1
2	Poeciliidae	<i>Priapichthys annectens</i>	1	1	1	0	0	0	0
2	Poeciliidae	<i>Priapichthys darienensis</i>	0	0	0	0	1	0	1
2	Poeciliidae	<i>Priapichthys panamensis</i>	0	1	0	1	0	0	0
2	Synbranchidae	<i>Synbranchus marmoratus</i>	1	1	1	1	1	1	1

Euclidean distances and Jaccard's similarity coefficient differed in the identification of drainage membership in biogeographical provinces, we examined the distribution of species' ranges across regions of high faunal turnover in order to resolve any inconsistencies between dendrograms regarding the placement of biogeographical boundaries. Moreover, we examined the data for drainages that may have been inappropriately assigned to a biogeographical province as a result of inadequate sampling of the fauna of that particular drainage. In general, when we deemed that drainages were positioned in an inappropriate cluster owing to inadequate sampling, we placed these drainages in a biogeographical province based on the geographical location of the drainage.

### Community composition, species richness, endemism, and range size

We calculated the relative community composition of biogeographical provinces by dividing the species richness of each freshwater fish family by the total number of species present in each biogeographical province, providing an estimate of the relative contribution of each family to the observed species richness for the province. Endemic species were defined as species whose global distributions are limited to one biogeographical province in the LMA region. The number of endemic species for each biogeographical province was divided by the species richness of the province to obtain a measure of the relative degree of endemism of each biogeographical province. The range size of LMA freshwater fishes was calculated by summing the number of biogeographical provinces occupied by each species.

### Beta-diversity

The relative permeability of dispersal barriers between biogeographical provinces was estimated by the specific covariance of occurrence between provinces. The specific covariance of occurrence (Bell, 2003) provides a standard method of expressing Whittaker's (1975) concept of beta-diversity and is defined as

$$\text{Cov}(X_{ij}, X_{ik}) = \frac{n_{11}n_{00} - n_{10}n_{01}}{N(N-1)},$$

where  $n_{11}$  is the number of species that occur at both sites (provinces in this article),  $n_{10}$  is the number of species that occur at site  $j$  but not at site  $k$ ,  $n_{01}$  is the number of species that

occur at site  $k$  but not at site  $j$ ,  $n_{00}$  is the number of species that do not occur at either of the sites, and  $N$  is the number of species in the survey (in this case, 170). Larger values of specific covariance between sites indicate greater faunal similarity, or decreased beta-diversity or turnover between the two sites.

## RESULTS AND DISCUSSION

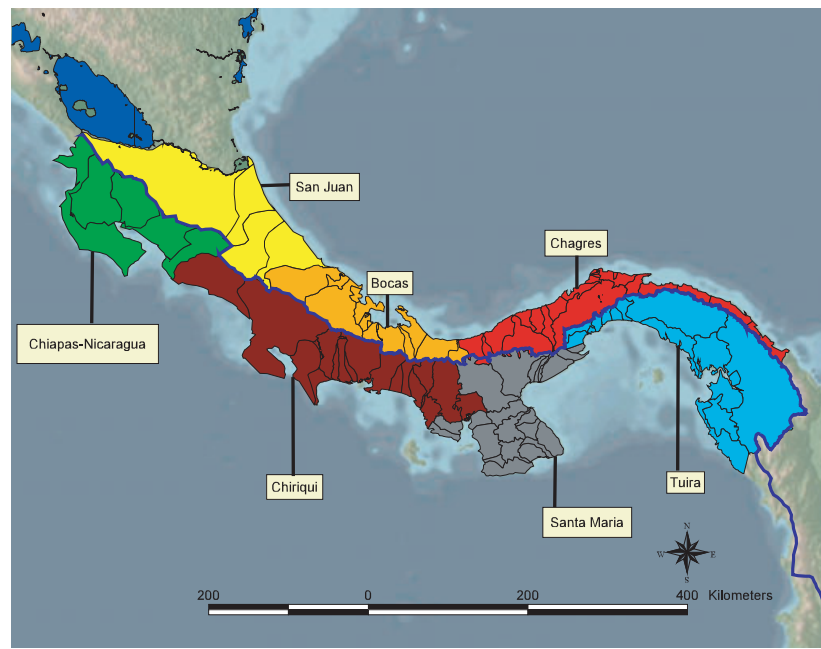
### Biogeographical provinces

The high degree of faunal turnover between the Rio Tuira in eastern Panama and the Rio Atrato in north-western Colombia (Loftin, 1965; Bermingham *et al.*, 1997a) suggests that the boundary between the countries, which follows the eastern limit of the LMA cordillera extending from the Caribbean to the Pacific coastline at the Colombian–Panama border (Fig. 1), is also an important biogeographical barrier. Furthermore, north-western Colombia has a history and ichthyofauna that predate the rise of the Isthmus of Panama (Coates *et al.*, 2004). At the other geographical extreme of LMA, a marine corridor existed in the region of Lake Nicaragua and the Rio San Juan well into the Pliocene (Coates & Obando, 1996), separating LMA from nuclear Mesoamerica near the current political boundary between Costa Rica and Nicaragua. Miller (1966) and Bussing (1976), however, hypothesized that the biogeographical provinces of both the Atlantic and Pacific slopes of Costa Rica continued northwards into Nicaragua (the San Juan and Chiapas-Nicaragua provinces, respectively), suggesting that the political border between Costa Rica and Nicaragua may not represent the northern terminus of the biogeographical provinces described herein.

We identified seven biogeographical provinces (Fig. 2), primarily based on convergent results of the UPGMA dendrograms (Figs 3 & 4). For the large majority of cases, both dendrograms yielded very similar results with respect to faunistic relationships between drainage basins and between areas. In addition, our cophenetic correlation analyses for UPGMA clusters based on Jaccard's similarity coefficient ( $r = 0.85$ ) and Euclidean distances ( $r = 0.83$ ) indicate that our UPGMA clusters represent a good fit to our data.

Nevertheless, several inconsistencies between the dendrograms exist. First, the dendrogram based on Euclidean distances clustered several drainage basins from the Tuira and Chagres provinces together. This depiction of the faunistic





**Figure 2** The biogeographical provinces of LMA. The faunistic relationships between LMA drainage basins were inferred based on concordance between methodologies and summarized to describe the biogeographical provinces of LMA freshwater fishes depicted in this figure.

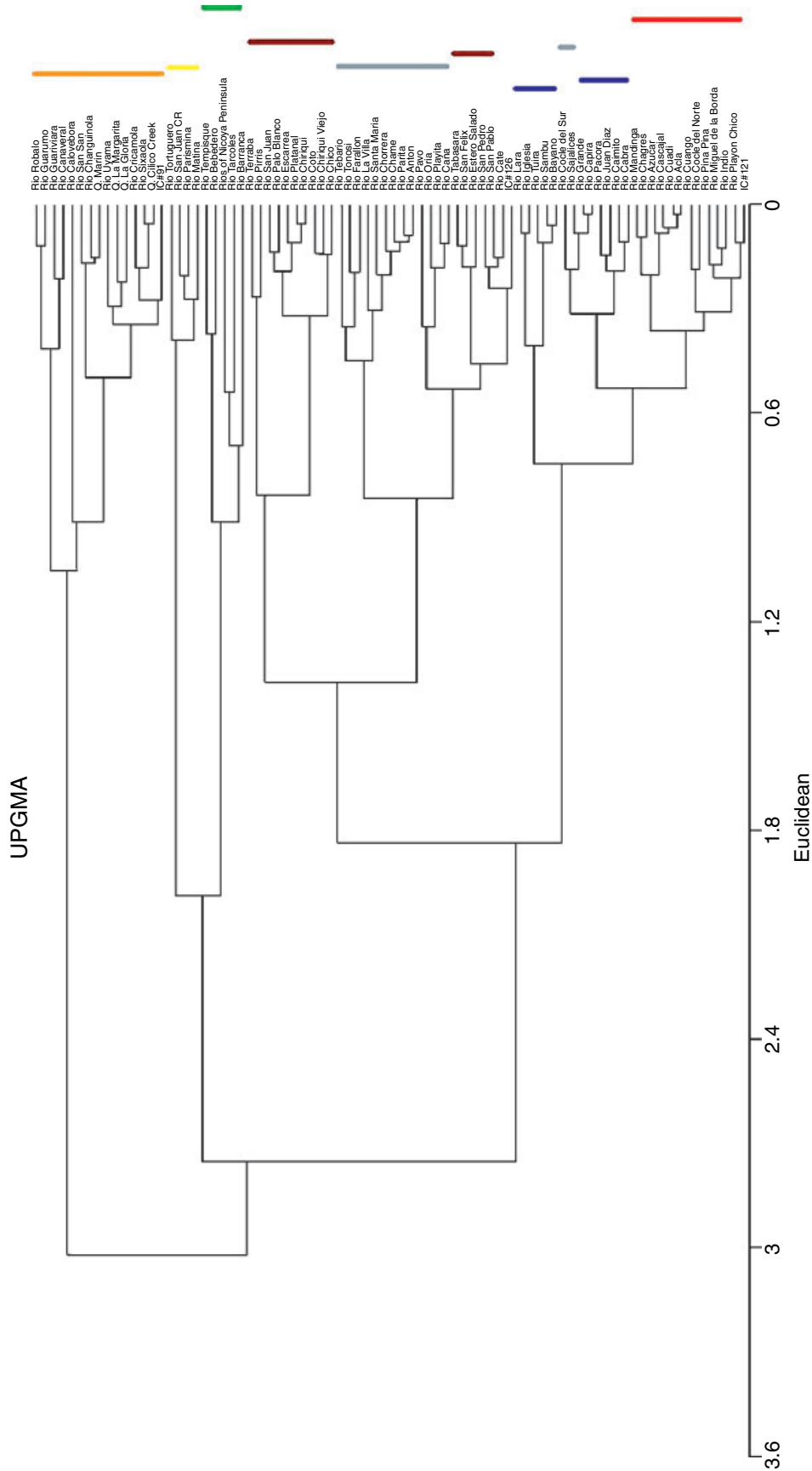
relationships between drainages differed from that based on Jaccard's similarity coefficient (Fig. 4), which placed the drainage basins of the Tuira and Chagres provinces in separate clusters. The clusters based on Euclidean distances (Fig. 3) reflect the faunal similarity of these rivers owing to the substantial number of shared species between the Tuira and Chagres provinces. In addition, the substantial number of species whose distribution is limited to the extremes of eastern Pacific Panama (the Tuira province) probably contributed to the relative dissimilarity among drainages within the Tuira province. We conclude, however, that the drainage basins on the Caribbean and Pacific slopes of eastern Panama represent discrete areas of faunal similarity and therefore qualify as separate biogeographical provinces (Fig. 4).

Furthermore, the dendrograms (Figs 3 & 4) identified different drainages separating the Santa Maria and Chiriqui provinces. This inconsistency clearly arises as a result of inadequate sampling of the Rio Playita, Rio Pavo, Rio Oria and Rio Cana drainage basins in the transitional area between provinces, as well as the natural decline in species richness along the Azuero Peninsula owing to a peninsular effect. Thus, we placed these drainages in biogeographical provinces based on the drainages' geographical locations. Finally, in cases for which the two dendrograms yielded differing descriptions of the faunal relationships between drainage basins and between areas, we also considered the distribution of species' ranges across province boundaries to settle inconsistencies between dendrograms. For example, based on the eight species whose westernmost distributions are located in the Rio Santa Maria, and the six species whose easternmost distributions are situated in the Rio Tabasara and the Rio San Pedro (three in each), we concluded that the boundary between the biogeographical provinces of the Chiriqui and Santa Maria provinces should be placed along the eastern edge of the Rio San Pablo

and the Rio San Pedro drainages (Fig. 4). The entire region, however, clearly represents an area of broad faunal turnover between the Santa Maria and the Chiriqui provinces.

Hugueny & Leveque (1994) point out that, because the dispersal of freshwater fishes often depends on direct connections between neighbouring rivers, the mean faunistic distance between drainage basins may be positively correlated with the geographical distance between drainages. Thus, it is critical to remove the variation that results from a drainage's geographical position. We therefore analysed our data using partial Mantel tests in order to remove the effect of the spatial positioning of the drainage basins, and found a significant correlation between the faunistic distances described in matrix  $x(y)$  and matrix  $x(z)$ . We conclude that the faunistic relationships did not arise solely as a result of the spatial arrangement of the drainage basins (Table 2). Rather, the results of the partial Mantel tests suggest that the clusters that we used to define the biogeographical provinces identified groups of drainages with shared biological history. Similar processes acting in the described biogeographical provinces have given rise to the observed faunal similarity among drainages within a province, and, therefore, patterns within the provinces can be used to illuminate the mechanisms responsible for the distribution and diversity of freshwater fishes at the landscape scale of LMA.

Previous attempts to describe the biogeographical provinces of the freshwater fish fauna of Mesoamerica led to the description of only four regions – the Chiapas-Nicaragua, Usumacinta, San Juan, and Isthmian provinces (Miller, 1966; Bussing, 1976). The reduced biogeographical resolution of these studies results from differences in the knowledge regarding the distribution of Mesoamerican fishes, and from the larger spatial scale at which their analyses were performed. For example, our results are based on more complete



**Figure 3** Dendrogram depicting the faunal relationships among LMA drainage basins as defined by a UPGMA cluster analysis based on the measure of Euclidean distances. The colours adjacent to the names of the drainages denote their respective biogeographical provinces (we used the same colour scheme as in Fig. 2). The biogeographical provinces (denoted by their colours in parentheses) are as follows: San Juan (yellow), Chiapas-Nicaragua (green), Bocas (orange), Chiriqui (maroon), Chagres (red), Santa Maria (grey) and Tura (teal).



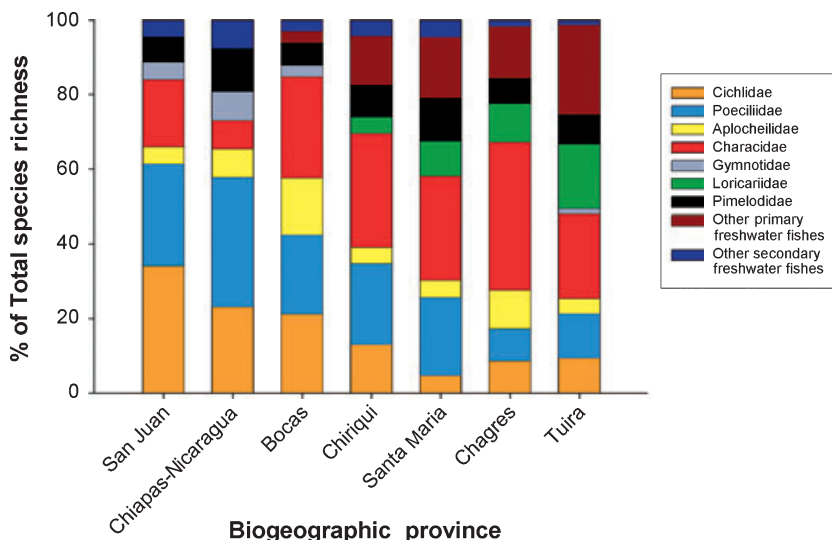
**Table 2** Results from two partial Mantel tests that were used to evaluate the significance of the faunistic relationships among LMA drainage basins established by UPGMA cluster analyses based on Euclidean distances and Jaccard's similarity coefficient. Three matrices were used for each of the two partial Mantel tests that were performed. Each partial Mantel test used a matrix that described the geographic distances between drainages to remove the effects of the spatial positioning of the drainages, and two matrices that described the faunistic distance/similarity between rivers based on the two sets of randomly defined species lists

Measure of faunal similarity/distance	<i>r</i>	No. of permutations	<i>P</i> -value
Euclidean distance	0.447	9999	< 0.0005
Jaccard's similarity coefficient	0.609	9999	< 0.0005

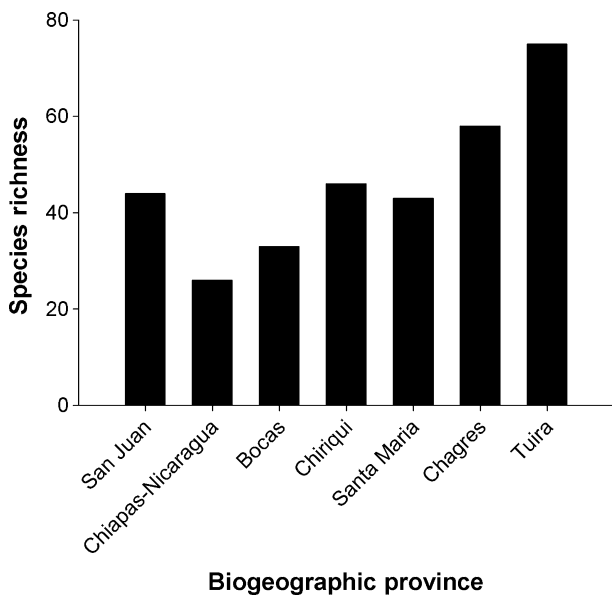
geographical sampling, and clearly demonstrate significant faunal turnover across the Isthmian province described by Miller (1966) and Bussing (1976). We define four discrete biogeographical provinces in this region: Chiriqui, Santa Maria, Tuira and Chagres (Fig. 2). In addition, Bussing (1976) locates the southern boundary of the San Juan province east of the Rio Calovebora, a result not supported by our data, which establish a faunal break between the Rio Matina and the Rio Sixaola drainage basins. Our analysis identifies a new biogeographical province in the region of Bocas del Toro encompassing the drainage basins between the Rio Calovebora and the Rio Sixaola (Bocas province), with the San Juan province to the north, probably extending to the Prinzapoloka drainage basin of Nicaragua, as previously asserted by Bussing (1976). The divide between the Rio Tarcoles and the Rio Pirris forms the biogeographical province of Chiapas-Nicaragua to the north, and the newly named Chiriqui province to the south. This boundary corresponds to that described by Miller (1966) and Bussing (1976) between their Chiapas-Nicaragua and Isthmian provinces.

### Community composition and species richness of LMA biogeographical provinces

Changes in community composition and to a lesser extent in species richness are striking as one travels east to west across the LMA landscape, reflecting changes in the relative contribution of primary versus secondary freshwater fishes. Species representing families of the secondary freshwater fishes Cichlidae and Poeciliidae have undergone substantial diversification and predominate in nuclear Mesoamerica, and this is reflected in the biogeographical provinces of north-western LMA (the San Juan, Chiapas-Nicaragua, and Bocas provinces, Fig. 5), whereas primary freshwater fishes are a considerably more prominent feature of south-eastern LMA communities. For example, Cichlidae and Poeciliidae constitute more than 60% of the San Juan fauna, whereas Characidae constitute only 18% of the total species richness of this province and Loricariidae are completely absent. In contrast, primary freshwater fishes of the Characidae family, and to a lesser extent of the Loricariidae family, contribute a much larger percentage of the total species richness of the south-eastern biogeographical provinces of LMA (the Chiriqui, Santa Maria, Chagres and Tuira provinces, Fig. 5). This trend is most clearly exemplified in the Chagres province, where Characidae and Loricariidae make up approximately 50% of the fauna, while Poeciliidae and Cichlidae represent only 17% of the total number of species present. However, changes in community composition across the LMA landscape are not mirrored by changes in the species richness of the biogeographical provinces. Species richness is highest at the eastern extreme of LMA, but does not decline smoothly as one travels west across the LMA, reflecting the counter-acting contribution of the diversification of the Cichlidae and Poeciliidae in north-western lower and nuclear Mesoamerica. This pattern is most clearly demonstrated by the increase in species richness in the San Juan and Chiriqui provinces (Fig. 6).



**Figure 5** The relative contributions of selected LMA freshwater fish families to the species richness of the LMA biogeographical provinces.



**Figure 6** Species richness of the biogeographical provinces of LMA.

Regional processes and biological differences among freshwater fish families played a central role in giving rise to the geographical variation in community composition across the LMA landscape. The emergence of the Isthmus of Panama over a period of 15 million years beginning in the mid-Miocene, coupled with episodes of sea-level regression, set the stage for the colonization of Mesoamerica by primary freshwater fishes (Miller, 1966; Myers, 1966; Bussing, 1976, 1985; Bermingham & Martin, 1998; Perdices *et al.*, 2002), and probably by secondary freshwater fishes as well (Murphy & Collier, 1996; Martin & Bermingham, 1998). In particular, several periods of geological development of the LMA landscape appear to have played important roles in determining the success of LMA freshwater fish colonists.

In the mid-Miocene, the region of present-day LMA was made up of a series of islands; marine connections between the Pacific and Caribbean were commonplace, and Central and South America were separated by an ocean barrier of abyssal-bathyal depths (> 2000 m) in the region of present-day eastern Panama and the Colombian Choco (Coates & Obando, 1996). There is no evidence that primary freshwater fishes colonized Mesoamerica during this time, but molecular analyses based on an mtDNA cytochrome *b* molecular clock suggest that heroine cichlids (Martin & Bermingham, 1998) and *Rivulus* (Murphy & Collier, 1996) arrived approximately 18–15 Ma (1–1.2% sequence divergence per Myr, Bermingham *et al.*, 1997b). How they did so is unknown. However, our presumption is that colonization was facilitated by some physiological tolerance of seawater.

There are many examples of salinity tolerance in cichlids; for example, the earliest fossil records of cichlids in South America in the Miocene strongly suggest that cichlids migrated from Africa to South America across the South

Atlantic via the South Equatorial Current (Murray, 2001), providing biogeographical evidence that cichlids are capable of crossing marine barriers. Furthermore, it is important to note when considering the dispersal of freshwater fishes across salt-water barriers that salinity levels of seawater may vary (Matthews, 1998). Lindsey & McPhail (1986) noted that temporary freshwater or brackish-water bridges can be formed in the sea during periods of high runoff, which may facilitate dispersal of freshwater taxa across oceanic gaps separating freshwater environments. It is therefore possible that salinity tolerance coupled with large flooding events associated with the northward discharge of the proto-Amazon in the region of the Magdalena river and Maracaibo basin (Lundberg *et al.*, 1998; Perdices *et al.*, 2002) provided the means for the Miocene colonization of Mesoamerica by secondary freshwater fishes, an event that pre-dated the final uplift of the Isthmus of Panama. The hypothesis of chance colonization during the Miocene is supported by molecular analyses: the phylogenies for heroine cichlids and *Rivulus* suggest that the colonization of Mesoamerica occurred once or no more than several times in each clade approximately 18–15 Ma (Martin & Bermingham, 1998).

Molecular analyses of extant taxa suggest that modern lineages of freshwater fishes did not colonize Mesoamerica prior to the mid-Miocene (Bermingham & Martin, 1998; Martin & Bermingham, 1998), and the fossil record does not suggest otherwise. Moreover, none of the North American primary freshwater fish families successfully colonized Mesoamerica south of Guatemala, and only the salt-tolerant Nearctic gars have managed to colonize as far south as the Great Lakes basin of Nicaragua and Costa Rica (Miller, 1966). Multiple lines of evidence therefore suggest that the streams and rivers of the LMA landscape very probably contained highly depauperate primary and secondary freshwater fish communities. Thus, we postulate that early LMA freshwater fish colonists encountered many empty ecological niches. Conditions during the mid-Miocene in nuclear Central America fostered an adaptive radiation among the Cichlidae and Poeciliidae in order to fill the 'ostariophysan vacuum' that existed in Mesoamerica at the time (Myers, 1966; Martin & Bermingham, 1998). This early radiation explains the relatively large contribution of Cichlidae and Poeciliidae to the species richness of northern LMA.

The continuing uplift of the Panamanian Isthmus, combined with the dramatically reduced sea level (Haq *et al.*, 1987) at the close of the Miocene, may have resulted in the ephemeral emergence of the Isthmus (Savin & Douglas, 1985) perhaps providing the earliest opportunity for the colonization of LMA by primary freshwater fishes (Bermingham & Martin, 1998). The Pliocene high sea-level stand would certainly have inundated the nascent Isthmus, causing extirpation and allopatric separation in central and eastern Panama. Local extinction events probably facilitated the subsequent colonization of freshwater fishes in this region, which may partially explain the relative richness of primary freshwater fishes in this region. Unlike the initial colonization of Mesoamerica by

secondary freshwater fishes, where the successful colonization of nuclear Central America was determined by hypothesized differences in salinity tolerance among freshwater fish families, the success of subsequent colonization events would have been primarily determined by the fishes' abilities to disperse across the landscape as well as by the conditions (distribution and diversity of fishes) of the putative source populations in north-western South America. The species richness of Characidae and Loricariidae in north-western Colombia far surpasses the species richness of other families of freshwater fishes (Table 3). These conditions clearly favoured colonization and subsequent allopatric diversification of the Characidae, and to a lesser extent of the Loricariidae, in eastern and central Panama, explaining the high species richness of primary freshwater fishes in south-eastern LMA.

The final closure of the Isthmus was completed approximately 3.5–3.1 Ma, serving to establish a permanent connection between north-western Colombia and eastern Panama, which in turn permitted the Great American Biotic Interchange across the LMA landbridge (Marshall *et al.*, 1979; Stehli & Webb, 1985; Coates *et al.*, 1992; Coates & Obando, 1996). Subsequent geological evolution of the LMA landscape resulted in the isolation of certain areas, which had important consequences for the dispersal and diversification of the fauna in these regions (Bermingham & Martin, 1998). For example, the rise of the Central Cordillera was an important vicariant event, which separated the faunas of the Caribbean and Pacific

**Table 3** Contribution of several freshwater fish families to the overall species richness of the Rio Atrato and Rio Magdalena drainage basins in north-western Colombia. We estimated the percentage contribution of several obligate freshwater fish families to the total species richness of the Rio Atrato and Magdalena drainage basins based on data contained in the NEODAT data base (<http://www.neodat.org>)

Freshwater fish family	Salinity tolerance	Percentage contribution
Characidae	1	35.2
Loricariidae	1	11.1
Aplocheilidae	2	2.7
Cichlidae	2	6.0
Poeciliidae	2	2.4
Synbranchidae	2	0.3

slopes of LMA (3–2 Ma, Collins *et al.*, 1995). Moreover, dispersal events of freshwater fishes were increasingly limited in their spatial extent as a result of the geological development of the LMA landscape (Bermingham & Martin, 1998). Thus, it is likely that, owing to geological processes, only the first colonization event of primary freshwater fishes reached the northern drainage basins of Costa Rica (Bermingham & Martin, 1998), leading to the disparity of the relative richness of primary and secondary fishes across LMA.

### Dispersal and speciation following the colonization of LMA

The relative importance of dispersal and speciation events in shaping patterns of distribution and diversity of LMA freshwater fishes following initial colonization varies across the spatial extent of LMA. Fifty-eight percent of the LMA ichthyofauna is endemic to LMA, suggesting that regional speciation has clearly played an important role in shaping patterns of diversity of the LMA freshwater fish fauna. Nevertheless, it is apparent that dispersal is a persistent aspect of the LMA biota.

Adjacent provinces along the same slope have exchanged faunas with increased frequency relative to provinces separated by the continental divide. Cross-cordillera turnover values of adjacent provinces were more pronounced than those of adjacent provinces along the same slope in 12 out of 18 cases (Table 4). This contrast in faunal turnover is probably the result of two general geological mechanisms: (1) river capture; and (2) river anastomosis across low-gradient palaeolandscapes. Both of these geological mechanisms certainly have larger impacts on adjacent drainages on the same slope for two principal reasons. First, drainage captures across a continental divide function to increase faunal similarity only to the extent that the fish species are likely to inhabit the captured reaches of the river. As Hildebrand (1938) noted, LMA rivers become increasingly depauperate with increasing elevation, thus precluding a large number of fish species from taking part in cross-Cordillera dispersal. Furthermore, Bishop (1995) indicated that the drainage rearrangements necessary for the dispersal of primary freshwater fishes across the landscape are rarer than biogeographers had previously speculated. In sum, river capture may rarely cause cross-cordillera faunal exchange

	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
San Juan	X						
Chiapas-Nicaragua	0.090	X					
Bocas	0.032		X				
Chiriqui	-0.023	0.029	-0.011	X			
Santa Maria			-0.002	0.079	X		
Chagres			-0.007		0.064	X	
Tuira					0.065	0.073	X

**Table 4** Specific covariation among the biogeographical provinces of LMA. The specific covariation metric is an estimate of beta-diversity, where larger values of the specific covariation indicate reduced species turnover between biogeographical provinces. We used the presence/absence of freshwater fish in the described biogeographical provinces to calculate these values

of any magnitude. Second, river anastomosis obviously has no impact on the faunal similarity of rivers on opposite sides of a continental divide, but figures importantly in the facilitation of faunal exchange among adjacent rivers along the same slope, particularly at reduced sea level in regions where the gradient of the continental slope is small.

An obvious exception to the general lack of cross-Cordillera faunal exchange regards the biogeographical provinces of San Juan and Chiapas-Nicaragua, marked by the lowest recorded value of species turnover (Table 4). This region is characterized by relatively low topography, and the traverse from the Rio Tempisque drainage basin (Pacific) across the Isthmus to the Rio San Carlos (part of the Rio San Juan drainage basin, Caribbean) does not rise above 45 m in altitude (Coates & Obando, 1996). The dispersal of freshwater fishes has obviously not been as strongly impeded between the San Juan and Chiapas-Nicaragua provinces in comparison with other areas in LMA where the Cordillera reaches much higher elevations and represents a more formidable barrier to fish dispersal. The faunal similarity between these provinces may also have been promoted by local extinction events, and subsequent re-colonization, associated with marine inundations of the southern Chiapas-Nicaragua province during interglacial periods (Haq *et al.*, 1987). Extinction can also be invoked to give a partial explanation of the low species richness and absence of endemic fishes in the Chiapas-Nicaragua province.

The Pacific slope of Panama, owing to the large number of shared species between biogeographical provinces, provides one of the clearest examples of facilitated dispersal among rivers along the same slope. 16 of the 25 species shared between the Chiriqui and the Santa Maria provinces are also shared with the Tuira province. The low degree of faunal turnover between Pacific slope drainages, coupled with the pattern of increasing faunal turnover from east to west, has several possible explanations. It is probable that the nascent Isthmus was characterized by relatively little topographic heterogeneity and thus by relatively large drainage basins with very similar faunas among Pacific coast biogeographical provinces. As the topographic complexity of the Isthmus increased, opportunities for river anastomosis and faunal exchange between some biogeographical provinces are likely to have decreased. For example, a coastal mountain chain bisecting the Santa Maria and Chiriqui biogeographical provinces developed in the region of the Sona peninsula. This peninsula extends close to the continental edge and thus there would have been little or no opportunity for rivers at the adjacent margins of the Chiriqui and Santa Maria provinces to anastomose across the exposed continental floodplain. Our analysis suggests, not surprisingly, that both the geographical description of biogeographical provinces, and the porosity of biogeographical barriers separating them probably changed over time. Furthermore, the relatively high endemism of Chiriqui province (30%) is probably a result of its increasing isolation over time. This view of landscape change over time, and the increasing evolutionary independence of the biogeographical provinces

along the Pacific slope, is supported by molecule-based phylogeographic analysis of widespread taxa across the LMA landscape (Bermingham & Martin, 1998; Perdices *et al.*, 2002).

Our results combined with molecular analyses (Bermingham & Martin, 1998) permit a strong inference that dispersal events resulting from river anastomosis occurring during periods of reduced sea level have had a large impact on the faunal similarity of the Santa Maria and Tuira provinces. Thirty species are shared by the Santa Maria and Tuira provinces, and the faunal turnover between these provinces is relatively low (Table 4). The increased likelihood of dispersal events in this region can in part be attributed to the low gradient of the continental shelf in the Bay of Panama (Loftin, 1965; Bermingham & Martin, 1998). The gradual decline of the continental shelf of the Bay of Panama combined with periods of reduced sea level during glacial maxima would have greatly facilitated fish dispersal through anastomizing lowland streams and swamps extending from the Rio Tuira to the streams of the Azuero Peninsula (Loftin, 1965; Bermingham & Martin, 1998). We modelled the distribution of streams in the Bay of Panama during the last glacial maxima using GRASS in order to examine how periods of reduced sea level during the last glacial maxima might have influenced the connectivity of present-day drainages. Our GIS modelling analysis (Fig. 7) suggests that many of the rivers that empty into the Bay of Panama were connected during the last glacial maxima; however, the spatial resolution of the data is not sufficient for us to present the palaeodrainage patterns with precision. Nevertheless, it is clear that geological processes facilitating dispersal between drainages in this area have had a large influence on the patterns of distribution and diversity observed in the Santa Maria and Tuira provinces. Our findings complement those of Bishop (1995), who suggested that the frequency of river captures is rarer than previously hypothesized by biogeographers. Our results indicate that river anastomosis during glacial maxima may occur more frequently and have a significantly larger impact on patterns of distribution and genetic divergence of freshwater fishes than the process of river capture.

The pan-Pacific dispersal corridor of central Panama stands in contrast to the relative isolation of Bocas province from adjacent provinces on the Caribbean slope (Table 4). Speciation has clearly had a large impact on patterns of distribution and diversity in this region: 42% of the fauna is endemic to the province (Fig. 8). Our analyses indicate that very strong dispersal barriers exist between the Bocas province and the ichthyological provinces along the same slope (the San Juan and Chagres provinces). The faunal assembly of the Bocas province may contain species (e.g. *Brachyhypopomus*; see Bermingham & Martin, 1998) derived from an early colonization event 7–4 Ma, followed by isolation from the rest of LMA approximately 3 Ma. The relative degree of isolation of the Bocas province from its Caribbean slope neighbours can be partly attributed to the gradient of the continental shelf in this area, which probably acted to reduce the frequency and extent of river anastomosis in this region relative to central Pacific Panama.



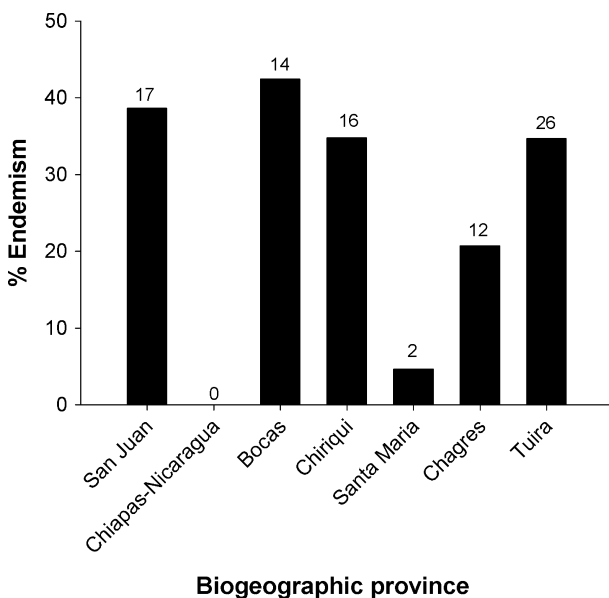


**Figure 7** Bathymetric streams of LMA during the last interglacial (sea level was set at  $-110$  m from present sea level). The bathymetric streams were modelled using the *r*. function of GRASS.

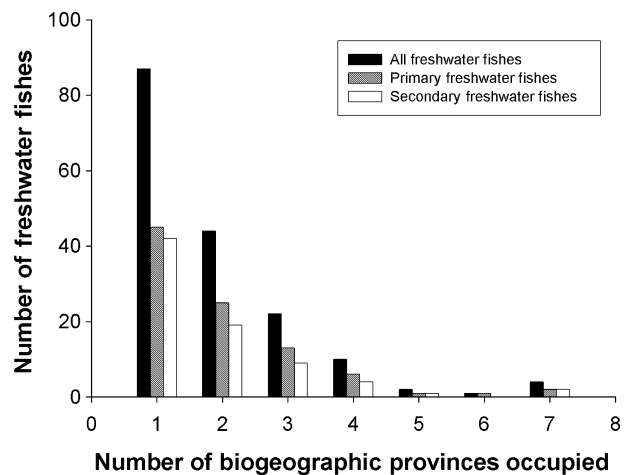
**Distribution of species ranges and dispersal limitation**

The distribution of range size for the freshwater fishes of LMA is geometric, whereby many more species have small ranges than large ranges (Fig. 9). This pattern is mirrored by the distribution of species ranges as a function of the number of

drainage basins occupied (data not presented). Hugueny (1990) reported a similar geometric distribution for the range size of Nilo-Sudanian freshwater fishes. Gaston (1994, 1996) has argued that the principal determinants of range-size distribution are habitat availability, habitat generalism, breadth of environmental tolerance and dispersal ability. The pattern of the geometric distribution of range size, however, has also been successfully reproduced by neutral community models in which the demographic properties of individuals are the same and dispersal gives rise to many of the macroecological patterns reported in the ecological literature (Bell, 2001; Hubbell, 2001). Dispersal limitation, whether it is as a manifestation of neutral



**Figure 8** Patterns of endemism in the LMA biogeographical provinces. The number of endemic species for each biogeographical province was divided by the species richness of the province to obtain a measure of the relative degree of endemism of each biogeographical province. The number above each of the bars indicates the number of endemic species located in each province.



**Figure 9** The distribution of range size (as measured by the number of biogeographical provinces occupied) for the freshwater fishes of LMA.



processes, or a function of the breadth of a species' environmental tolerances and the corresponding distribution of habitat across the landscape, or some combination thereof, is probably responsible for the observed patterns of range-size distribution of LMA freshwater fishes.

Given dispersal limitation, it would seem to follow that secondary freshwater fishes would have larger range sizes than primary fishes as a result of the increased salinity tolerance posited for the former group, and thus an increased probability of dispersal along coastlines. However, the average range sizes of primary and secondary freshwater fishes are not significantly different ( $t$ -test,  $P = 0.54$ ), suggesting that these fishes experience similar constraints on dispersal. The range-size distribution of both primary and secondary freshwater fishes follows a geometric curve similar to that observed for the combined plot of species ranges across the LMA biogeographical provinces (Fig. 9). Many more species of both primary and secondary freshwater fishes therefore have smaller ranges than larger ranges. The small average range size of both primary and secondary freshwater fishes indicates that dispersal along coastlines must be a fairly infrequent event and that the differential salinity tolerance hypothesized to distinguish primary freshwater fishes from secondary freshwater fishes is not an important determinant of range size. Hugueny (1990) also rejected the hypothesis that secondary freshwater fish species have larger ranges and are less dispersal-limited than primary fishes for the Nilo-Sudanian freshwater fish fauna.

These results call into question the salinity tolerance of primary and secondary freshwater fishes, which has never been experimentally verified. However, there is no escaping the observation that the distribution of the vast majority of primary freshwater fishes is limited to the freshwaters of continents and continental islands, whereas the distribution of secondary freshwater fishes includes many islands that have not had continental connections during the Cenozoic (West Indian islands, Madagascar, the Seychelles, etc., Myers, 1949). Resolution of this apparent paradox would suggest that, whereas fishes of some freshwater fish families encountered in Mesoamerica, for example the Characidae and the Pimelodidae, are unlikely ever to cross marine barriers, others such as the Cichlidae and Poeciliidae are physiologically capable of doing so, but do so only rarely. The hypothesis of rare marine dispersal posits a high probability of monophyly in groups that have crossed marine barriers to colonize new landscapes. This prediction appears to be largely met by the Heroini (Cichlidae) found in Mesoamerica and the Greater Antilles (Martin & Bermingham, 1998; G. A. Concheiro *et al.*, unpubl. data). Additional phylogenetic analysis as well as sophisticated physiological experimentation of the salinity tolerance and adaptive potential of Neotropical freshwater fishes are required to determine how variable this trait is within and between families. More detailed analysis of Myers's (1949) intelligent and provocative deduction regarding salinity tolerance differences in freshwater fishes based on the biogeographical distribution of freshwater fish families is warranted, given the enormous importance of his ideas for the interpretation of fish dispersal probability, and, in turn, Earth history.

## CONCLUSION

Our study clearly indicates that regional processes had an important influence on the assembly of the LMA freshwater fish fauna and that, in particular, the process of dispersal probably plays an ongoing role in the maintenance of LMA freshwater fish assemblages. This observation has important ramifications for both theory and conservation. Our results suggest that the study of regional processes is essential to explaining patterns of biological diversity. Biogeographical analyses of regional faunas at large spatial scales coupled with phylogeographic analyses that elucidate regional colonization history will certainly provide further insight into the processes that determine patterns of biodiversity. Biogeographical studies paint the backdrop upon which local interactions play themselves out, permitting inference regarding the relative importance of local and regional processes in shaping the diversity and structure of ecological communities. This observation lends support to the importance of a top-down approach to the study of species richness and diversity (Tonn *et al.*, 1990; Ricklefs & Schluter, 1993; Whittaker *et al.*, 2001).

Freshwater faunas are among the most threatened taxa on the planet (Ricciardi & Rasmussen, 1999). However, conservation efforts in areas such as LMA have suffered from a scarcity of large-scale descriptions of biodiversity patterns capable of informing conservation decisions. Our analyses identify areas of high faunal endemism and species richness of the LMA freshwater fish fauna. These areas are of high conservation value and provide a baseline for informing conservation strategies in LMA. Similar studies of other organisms in this area and across the globe will provide important information for conservation planners and policy makers alike.

Our results also emphasize the importance of designing conservation strategies that permit the continued influence of regional processes on patterns of local diversity. The importance of dispersal in maintaining species richness over ecological and geologic time-scales via rescue effects (Brown & Kodric-Brown, 1977) suggests that the maintenance of dispersal corridors between areas of suitable habitat both within and among drainage basins should be an important conservation priority. Drainage basins that are increasingly isolated are more susceptible to local extirpation (or extinction if the species is endemic to the drainage basin) and less likely to receive colonizers (Olden *et al.*, 2001). We conclude, therefore, by calling for conservation planning and action that acknowledges the importance that regional processes play in determining patterns of biological diversity and that incorporates these processes in our strategies to conserve remnant biodiversity.

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## BIOSKETCHES

**Scott A. Smith** is currently pursuing his research interests in a PhD program in the Department of Biology at McGill University, where he is studying the nature of invasion and its impacts on community structure, as well as the effects of human modification of the environment on the functioning of ecological systems. The research for this paper was conducted during the completion of Scott's Master's degree under the auspices of the Neotropical Environment Option (NEO), and was carried out jointly at the Department of Biology of McGill University and the Smithsonian Tropical Research Institute.

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