The importance of regional and historical processes in the assembly and maintenance of lower Mesoamerican freshwater fish communities

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February 2004.

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science.

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Abstract

The relative importance of local, regional and historical processes to patterns of distribution and diversity of lower Mesoamerican (Panama and Costa Rica, LMA) freshwater fishes are examined at two different spatial scales. Biogeographic patterns of LMA freshwater fish communities at the spatial extent of LMA indicate that biological differences among species as well as regional and historical processes are quintessential to explaining the patters of turnover of community composition and species richness across the LMA Isthmus. The study of LMA freshwater fishes permits the inference that ecological interactions among species are not independent of a region's history, suggesting that regional and historical processes probably play an ongoing role in the maintenance of LMA freshwater fish communities. In addition, the study of the natural experiment of the Panama Canal provides a clear demonstration that dispersal, rather than local deterministic processes such as competition and predation, previously set the upper limit of the number of fish species coexisting in local communities. Comparisons of species inventories established prior to Canal construction with contemporary species lists demonstrates a large net increase in species richness of local communities, suggesting that the local communities of the Panama Canal watershed were not saturated.

Résumé

L'importance relative des processus locaux, régionaux et historiques sur la distribution et la diversité des poissons d'eaux douces du bas-mesoamericain (Panama et Costa Rica, LMA) sont examinés à deux différents niveaux spatiaux. La distribution biogéographique des communautés de poissons d'eaux douces, examinée à l'étendue du LMA indique que les différences biologiques entre les espèces ainsi que les processus régionaux et historiques sont d'une grande importance pour expliquer le revirement de la composition des communautés et la richesse biologique à travers le LMA. L'étude des poissons d'eaux douces du LMA mène à la conclusion que les interactions écologiques entre les espèces ne sont pas indépendantes de l'histoire de la région. Cela suggère que les processus régionaux et historiques jouent probablement un rôle actif dans la maintenance des communautés de poissons du LMA. De plus, l'étude de l'expérience naturelle qu'est le Canal de Panama démontre clairement que la dispersion, et non les processus locaux comme la compétition entre espèces ou la prédation, a antérieurement établit le niveau limite du nombre d'espèces de poissons d'eaux douces pouvant survivre ensemble dans les communautés locales. La comparaison des inventaires d'espèces établit avant la construction du Canal de Panama avec les listes contemporaines d'espèces démontre une importante augmentation de la richesse des communautés locales, suggérant que les communautés locales du bassin hydrographique du Canal de Panama n'étaient pas saturées auparavant.

Acknowledgements

I would like to thank the Natural Science and Engineering Research Council (NSERC) of Canada who graciously provided the funding for my Master's project through a PGS A scholarship. The Smithsonian Tropical Research Institute (STRI) provided logistical and financial support during my many adventures in Panama. I would also like to thank all of the administrative personnel and faculty at McGill University and STRI that made participation in the NEO option both possible as well as such an enjoyable and educationally rewarding experience.

Preparation of the databases that I used for the analyses conducted in the first chapter of my thesis was greatly aided by Rigoberto Gonzalez, who provided apt and timely advice regarding the distribution of lower Mesoamerican freshwater fishes. Dr. Oris Sanjur provided countless advice regarding the use of both Microsoft Excel and FileMaker Pro. The field work that I undertook as part of my second chapter would not have been possible without an enormous amount of help from the following people, to whom I am greatly indebted: Luis Fernando de Leon, Rigoberto Gonzalez, Neilan Kuntz, Jacqueline Loo, Dr. Anabel Perdices, Gisela Reina, Dr. Oris Sanjur, and especially Andrew Moeser. The Autoridad Nacional del Medio Ambiente (ANAM) and the Autoridad de la Region Interoceanica (ARI) in Panama kindly provided the required sampling and access permits.

Professor Graham Bell co-supervised my thesis and provided timely and astute advice during the planning of the second chapter of my thesis. Our idea to survey the fishes of the Panama Canal area and compare contemporary and historical records could not have turned out any better. Graham provided outstanding editorial advice during the preparation of the manuscript presented in Chapter #2. Furthermore, time spent in the Bell lab helped me develop a greater appreciation for the experimental approach to ecology and evolution.

Dr. Eldredge Bermingham's patience and teaching abilities enabled me to grow enormously as a graduate student. Serving as the main supervisor of my first thesis chapter and as a co-supervisor of my second chapter, Biff provided outstanding support in all of the endeavors that I undertook during my Master's, ranging from database preparation, to experimental design and all the way through the actual writing and editing portion of my Master's. I am especially indebted to Biff for the time and care that he put into editing both of my thesis chapters. I am, hopefully, a much better writer as a result of his countless efforts to teach me the so called tricks of the trade.

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General Introduction

The study of the spatial distribution of biological diversity is of grand interest to community ecologists and biogeographers. The relative importance of the processes responsible for the generation and maintenance of this diversity, however, remain elusive. Identifying the relative contribution of local, regional and historical processes to the species richness and composition of local communities may provide a key to understanding global patterns of species richness (Huston 1999, Gaston 2000). Studies that have examined the importance of processes operating at spatial scales larger than the scale at which organisms interact have been extremely limited as a consequence of the limited availability of large-scale datasets as well as the difficulty in experimentally manipulating processes acting at large spatial scales. The scale of ecological experimentation has changed very little since Darwin's experimentation on the decomposition of organic material by earth worms (Darwin 1888, Gaston 2003). Ecologists have tended to focus their attention on mechanisms that operate at very small spatial scales; the spatial scales at which their own senses principally function (Gaston 2003). The focus of community ecologists on processes operating at the scale of local communities has led to the conclusion that local processes such as competition, predation and parasitism are of prime importance to the patterns of distribution and diversity of organisms that we observe in nature (Ricklefs 1987, 1989, Cornell 1999). Ricklefs (1987), however, underlined the importance of regional and historical processes in the assembly and maintenance of biological communities. Furthermore, some authors have suggested that local communities are assembled from a regional pool of species, whose species richness and distribution is determined by the regional and historical processes unique to a given area (Gaston 2000). Clearly, the relative importance of local and regional processes depends on whether species are generally excluded from sites by local deterministic processes (Diamond 1975, Shurin 2000) or by dispersal limitation (Sale 1977, Bell 2001, Hubbell 2001).

In order to understand the relative importance of local, regional and historical processes to the patterns of species richness and community composition that we observe in nature, studies at various spatial scales are necessary to decipher amongst the relative importance of these processes (Lawton 1999). For example, the processes responsible for continental patterns of the distribution and diversity of organisms can only be understood through the examination of databases that document the distribution of organisms at the continental scale. In the following chapters, I examine the processes responsible for the patterns of distribution and diversity of lower Mesoamerican (Panama and Costa Rica, LMA) freshwater fishes at two very different spatial scales.

Two important facts suggest that the study of the patterns of diversity and distribution of Mesoamerican freshwater fishes at the continental scale will permit inferences regarding the importance of regional and historical processes in the assembly and maintenance of biological communities. First, the isthmian corridor provided the first opportunity for primary South American freshwater fishes to colonize Mesoamerica during the Pliocene (Myers 1966, Bermingham and Martin 1998), and thus the evolutionary assembly of LMA freshwater fish fauna is recent, simplifying its study. Second, the dispersal of primary (and to some extent, secondary) freshwater fishes is dependent on direct connections between rivers, and thus, drainage basins function as terrestrial islands that create repeated patterns of subdivision of populations and communities within discrete boundaries. The dispersal constraints of freshwater fishes facilitate the description of the faunal relationships among drainage basins, in addition to the characterization of the importance of regional and historical processes on the assembly and maintenance of the LMA freshwater fish fauna.

In the first chapter of this thesis, I examine the biogeographic patterns of the LMA freshwater fish fauna using a database that records the presence and absence of primary and secondary freshwater fishes in drainage basins across the LMA landscape. Patterns of community composition, species richness and endemism are documented in order to examine how regional and historical processes have influenced the diversification history of the Mesoamerican freshwater fish fauna. In addition, I document the relative permeability of geographic barriers to dispersal by quantifying the biological turnover between biogeographic provinces and assess the range size distribution of the LMA freshwater fishes, thus providing insights into how biological and historical processes have affected the dispersal of Mesoamerican freshwater fishes.

In the second chapter of this thesis, I document the outcome of the natural experiment that occurred following completion of the Panama Canal. The serendipity of having the natural experiment of the Panama Canal located within the middle of previously defined study area of lower Mesoamerica is truly quite remarkable and presents a unique opportunity to inform the conclusions presented in Chapter #1. Moreover, natural experiments probably provide the best means for investigating the relative importance of local versus regional processes, as well as documenting the degree of saturation of local communities, but experiments of appropriate scale are rare. In such cases regional diversity is disturbed, and the change in local species richness over time is documented (Ricklefs and Schluter 1993, Caley and Schluter 1997, Cornell 1999).

Completion of the Panama Canal in 1914 breached the continental divide permitting freshwater fish communities isolated on the Pacific and Caribbean slopes to come into contact, thus setting into motion a natural experiment of unprecedented proportion. The construction of a freshwater dispersal corridor between Pacific and Caribbean drainage basins dramatically increased the likelihood of dispersal between evolutionarily isolated communities, while maintaining all other variables constant within their natural range of variation, permitting strong inference regarding the importance of dispersal in setting the upper limit to the number of species that can coexist in local communities. Comparisons of species inventories established prior to Canal construction with contemporary species lists enable the evaluation of the state of saturation of the drainage basins of the Panama Canal watershed.

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Chapter #1: The Biogeography of lower Mesoamerican Freshwater Fishes

The Biogeography of lower Mesoamerican Freshwater Fishes

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ABSTRACT

Aim This paper seeks to examine the importance of regional and historical 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.

Methods The biogeographic provinces of lower Mesoamerica (LMA) were described using presence/absence data of primary and secondary LMA freshwater fishes. Subsequent analyses were undertaken at the spatial resolution of the biogeographic provinces and sought to describe patterns of community composition, species richness, endemism, range size, and the permeability of dispersal barriers between biogeographic provinces, which was quantified using the specific covariance of occurrence between provinces.

Results Changes in community composition and species richness across lower Mesoamerica clearly highlight the importance of biological differences among freshwater fish species in shaping the patterns of distribution and diversity observed at the continental scale lower Mesoamerica, providing clear evidence of non-neutral patterns at large spatial scales. Patterns of endemism and turnover between biogeographic provinces suggest differential importance of dispersal and in situ speciation events in shaping patterns of freshwater fish diversity across lower Mesoamerica. Moreover, the distribution of range size of LMA freshwater fishes indicates that these organisms are extremely dispersal limited and that dispersal events along coastlines of both primary and secondary freshwater fishes must be extremely infrequent.

Main conclusion Diversity anomalies in matched communities in different regions provide one of the best lines of evidence that history imparts a powerful imprint on the composition and species richness of local communities. Our results establish that history has a primary influence on the distribution and diversity of biological communities, and that the ecological interactions among species are not independent of a region's history. The interactions among species in any given community are defined by the historical events responsible for the assembly of that fauna. Thus, our study shows that regional and historical processes play an ongoing role in the composition of freshwater fish communities.

INTRODUCTION

Identifying the relative contribution of local, regional and historical processes to the composition and species richness of local communities provides a key to understanding global patterns of 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, however, the role of regional (dispersal, speciation and extinction) and historical (age, geology, size and the climate of a region) processes in the assembly and maintenance of biological communities has been emphasized (Ricklefs 1987, Ricklefs and Schluter 1993, Gaston 2000, Gaston 2003, Mora et al. 2003).

A well documented example of the importance of historical processes is the Pliocene completion of the Isthmus of Panama, which connected the South and North American continents permitting a massive exchange of flora and fauna, an event termed the Great American Interchange (Marshall et al. 1979, Stehli and Webb 1985). The specific consequences of this event for freshwater fish have been described by a variety of investigators (Myers 1966, Miller 1966, Bussing 1985, Bermingham and Martin 1998). More specifically, several authors have noted that both the primary and secondary freshwater fish faunas of Mesoamerica were derived from putative source populations in northwestern Colombia (Myers 1966, Miller 1966, Bussing 1976, Bussing 1985, Bermingham and Martin 1998, Martin and Bermingham 1998, Perdices et al. 2002, Reeves and Bermingham unpublished data), and that the emerging Isthmus provided differential colonization opportunities for these fishes. Secondary freshwater fishes such as cichlids and aplocheilids colonized Mesoamerica between 18-15 Ma, approximately 10 Ma earlier than primary freshwater fishes (Bermingham and Martin 1998, Martin and Bermingham 1998), according to molecular clock estimates. This backdrop provides an interesting setting for understanding the processes that regulate patterns of distribution and diversity of organisms at the continental scale.

Two important facts suggest that the study of the patterns of distribution and diversity of LMA (Lower Mesoamerican) freshwater fishes will permit inferences regarding the relative role that regional and historical 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 fishes in Mesoamerica (Myers 1966, Miller 1966, Bussing 1985), recent molecular systematic research indicates that the evolutionary assembly of the LMA freshwater fish fauna is recent (Bermingham and Martin 1998, Perdices et al. 2002, Reeves and Bermingham unpublished data), suggesting that the historical record of colonization is largely intact because it is not likely to have been overwritten by multiple rounds of dispersion. Second, drainage basins function as terrestrial islands that create repeated patterns of subdivision of populations and communities within discrete boundaries. These patterns arise largely as a result of the dispersal constraints of obligate freshwater fishes. Primary freshwater fishes are hypothesized to be physiologically intolerant of saline conditions and thus cross marine barriers with great difficulty (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 physiographic changes of the land, river anastomosis during periods of reduced sea-level (which occur during glacial maxima) as well as during high water of the rainy season, and perhaps pulses of freshwater into the ocean that occur during flood events in watersheds (Myers 1938, 1966, Miller 1966, Loftin 1965, Bermingham and Martin 1998, Unmack 2001). Secondary freshwater fish, however, can tolerate moderate levels of salinity and may be able to disperse along coastlines, although the frequency of such colonization events remains unknown.

A first step towards studying the importance of regional and historical processes is adequate faunal description of biogeographic provinces. Biogeographic provinces represent geographic regions of relative homogeneous faunal composition and their description permits analysis of the processes responsible for turnover, both in terms of species richness and community composition. We test whether changes in faunistic similarity among drainage basins result simply from the spatial arrangement of the rivers and the source of colonists or from particular geographical features of the landscape and the idiosyncratic biology of the fish. In turn, we evaluate patterns of community composition, species richness and endemism at the scale of biogeographic provinces to document physiological, regional and historical influences on the dispersal and diversification history of the Mesoamerican freshwater fish fauna. Furthermore, we use an estimate of beta diversity in order to quantify the biological turnover between biogeographic provinces and, thus, to estimate the relative permeability of geographic barriers to dispersal. Lastly, we assess the range size distribution of the LMA freshwater fishes by determining the number of biogeographic provinces occupied by each species and test whether hypothesized differences in salinity tolerance between primary and secondary fishes have influenced the sizes of the geographic ranges of these fishes.

METHODS

Data Sources

We focused our analyses on the LMA region, which we define to include all the rivers of Panama and Costa Rica (Fig. 1). We assembled a database describing species' presences and absences throughout LMA based on information of species distribution contained within the NEODAT database and the Smithsonian Tropical Research Institute (STRI) Freshwater Fish Collection (Bermingham et al. 1997a). The records were geo-referenced and each record's merit for analytical use was verified using the literature and the STRI Freshwater Fish Collection. Only collection records for primary and secondary freshwater fishes were used in the 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 almost certainly owed to insufficient samples. But owing to the fairly dense sampling of rivers across the isthmian landscape, absence of a fish species at the provincial level was assumed to be real. Since all of our analyses were undertaken at the provincial level, the inferences that we make regarding the importance of regional and historical processes in explaining the patterns of distribution and diversity of the LMA freshwater fishes 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 *Roeboides* (Bermingham and Martin 1998) uncovered phylogenetic variation that made geographic sense of a bewildering distribution pattern based on the preceding taxonomy and led to the description of three new species (Lucena pers. comm.). That said we are confident that our description of both taxa and geographic distributions is largely correct owing to molecule-based phylogeographic analyses of most potentially problematic taxa (Bermingham and Martin 1998, Martin and Bermingham 2000, Perdices et al. 2002, Reeves and Bermingham unpublished data).

Biogeographic provinces

Correspondence analysis was used to convert the binary species presence/absence data into continuous variables (Jackson and Harvey 1989, Hugueny and 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 and Legendre 1998) and thus simplifies the recovery of meaningful patterns in early 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 biogeographic perspective (Hugueny and Leveque 1994). Correspondence analysis is preferred over other methods of multivariate analysis because it is based on a metric that does not include cases where two species are both absent in a locality in its computation (Hugueny and Leveque 1994), and is thus strongly recommended for ecological or biogeographic multivariate analyses that rely on binomial data (Legendre and Legendre 1998).

Next, the Euclidian distance coefficient (ED) was used to compute the faunistic distances between the rivers based on the coordinates representing the first three axes of the correspondence analysis. Unweighted Pair Group Method with Arithmetic mean (UPGMA) analysis was used to produce a dendogram 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 and did not involve the use of correspondence analysis to initially transform the data. UPGMA cluster analysis was performed in order to produce a dendogram describing the faunistic relationship between drainage basins based on Jaccard's similarity coefficient (all of the aforementioned procedures were implemented in MVSP v3.1).

Following the methodology of Bernard Hugueny and Pierre Legendre (pers. com.), a partial Mantel's tests was used to test the significance of the faunistic relationships among drainage basins (R Package v 4.0). The data were first partitioned into two randomly defined groups of species (y and z). In turn, we used 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, www.jennessent.com) was used to calculate the geographic distance between each of the drainage basins, resulting in a third matrix, the geographic distance matrix. A partial Mantel's test was then performed on the faunistic distance matrices, using the geographic distance matrix to remove the effect of the spatial positioning of the drainage basins. The partial Mantel's test determined whether the faunistic relationships between the two faunistic similarity matrices are in fact meaningful. A second partial Mantel's test was conducted using the prescribed methodology, however, we substituted Jaccard's similarity coefficient with measures of Euclidean distances to describe the faunistic relationships between drainages based on the two sets of randomly defined species lists.

Community composition, species richness, endemism, and range size

We calculated the relative community composition of biogeographic provinces by dividing the species richness of the primary freshwater fish families Characidae, Loricariidae, Pimelodidae and Gymnotidae, as well as those of the secondary freshwater fish families Cichlidae, Poeciliidae and Aplocheilidae by the total number of species present in each biogeographic province, providing an estimate of the relative contribution of each family to the observed species richness. We calculated the species richness of each of the LMA biogeographic provinces by summing the total number of species that occurred in each province. Endemic species were defined as species whose global distributions are limited to one biogeographic province in the LMA region. We summed all of the endemic species for each biogeographic province and divided this number by the species richness of the province in order to obtain a measure of the relative degree of endemism of each biogeographic province. The range size of LMA freshwater fishes was calculated by summing the number of biogeographic provinces occupied by each species, and mean range sizes of primary and secondary freshwater fishes were used to investigate the influence of salinity tolerance on dispersal ability.

Beta-diversity

The relative permeability of dispersal barriers between biogeographic provinces was estimated by the specific covariance of occurrence between provinces. The specific covariance of occurrence (Bell pers. com.) provides a standard method of expressing Whittaker's (1970) concept of beta-diversity and is defined:

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

where n_{11} is the number of species that occur at both sites (or provinces), 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 and 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.

Moreover, we modeled the distribution of streams in the Bay of Panama during the last glacial maxima using GRASS in order to examine how changes in sea-level during periods of reduced sea-level during glacial maxima might have influenced the connectivity of present-day drainages.

RESULTS AND DISCUSSION

Biogeographic Provinces

Although LMA is defined by political borders, the high degree of faunal turnover between the Rio Tuira in eastern Panama and the Rio Atrato in northwestern Colombia (Loftin 1965, Bermingham et al. 1997a) indicates that the Panamanian-Colombian border is a natural boundary to the dispersal of freshwater fishes. At the other geographic extreme of LMA, a marine corridor existed in the region of Lake Nicaragua and the Rio San Juan well into the Pliocene (Coates and 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 biogeographic provinces of both the Atlantic and Pacific slopes of Costa Rica continued northward into Nicaragua (the San Juan and Chiapas-Nicaragua provinces, respectively), suggesting that the political border between Costa Rica and Nicaragua is not a true biogeographic boundary.

We identified 7 biogeographic provinces (Fig. 2) primarily based on convergent results of the UPGMA dendograms based on Euclidean distances (Fig. 3) and Jaccard's similarity coefficient (Fig. 4). For the large majority of cases, both dendograms yielded very similar results with respect to faunistic relationships between drainage basins and among areas. However, several inconsistencies between dendograms exist. First, the dendogram based on Euclidean distances clustered several drainage basins from the Tuira and Chagres provinces together. This depiction of the faunistic relationships among 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 extremities of eastern Pacific Panama (the Tuira province) probably contributed to the relative dissimilarity among drainages of the Tuira province. We conclude, however, that the drainage basins of eastern Caribbean and Pacific Panama represent discrete areas of faunal similarity and qualify as separate biogeographic provinces (Fig. 4). Furthermore, the dendograms (Figs. 3 & 4) suggest different areas of importance for the transition area separating the Santa Maria and Chiriqui provinces. These inconsistencies clearly arise as a result of the undersampling of the Rio Playita, Rio Pavo, Rio Oria and Rio Cana drainage basins, as well as the natural decline in species richness along the Azuero Peninsula owing to a peninsular effect. In general, when we deemed that drainages were positioned in an inappropriate cluster owing to undersampling, we placed these drainages in the appropriate biogeographic province based on the drainages' geographic location. Finally, in cases where the two dendograms yielded differing descriptions of the faunal relationships between drainage basins and among areas, we also considered the distribution of species' ranges across province boundaries to settle inconsistencies between dendograms. For example, based on the eight species whose westernmost distributions are located in the Rio Santa Maria, and the 6 species whose easternmost distributions are situated in the Rio Tabasara and the Rio San Pedro (3 respectively), we concluded that the boundary between the biogeographic 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.

To determine if the faunal relationships depicted in the dendograms are greater than would be expected by chance, we analyzed the data using partial Mantel's tests to remove the effect of the spatial positioning of the drainage basins. Hugueny and Leveque (1994) point out that owing to the fact that the dispersal of freshwater fishes often depends on direct connections between neighboring rivers, it is reasonable to assume that mean faunistic distance between drainage basins would be positively correlated with the geographic distance between drainages. Thus it is critical to remove the variation that results from a drainage's geographic position. We found a significant correlation between the faunistic distances described in matrix x(y) and x(z), and conclude that the faunistic relationships did not arise solely as a result of the spatial positioning of the drainage basins (Table 1), suggesting that the biogeographic provinces described herein are in fact biologically meaningful.

Previous attempts to describe the biogeographic 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 biogeographic resolution of these studies results from differences in the knowledge base regarding the distribution of Mesoamerican fishes, and to the larger spatial scale at which their analyses were performed. For example, our results are based on more complete geographic sampling, and clearly demonstrate significant faunal turnover across the Isthmian province described by Miller (1966) and Bussing (1976). We therefore define four discrete biogeographic provinces in this region: Chiriqui, Santa Maria, Tuira and Chagres (Fig. 2). Regarding the San Juan province, Bussing (1976) locates the southern boundary east of the Rio Calovebora, a result not supported by our data, which establishes a faunal break between the Rio Matina and the Rio Sixaola drainage basins. Our analysis identifies a new biogeographic 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 asserted by Bussing (1976). The divide between the Rio Tarcoles and the Rio Pirris forms the biogeographic provinces 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 the Isthmian provinces.

Historical processes, community composition and species richness of LMA biogeographic provinces

Changes in community composition and to a lesser extent species richness are striking as one travels east to west across LMA. The change in community composition across LMA owes to changes in the relative contribution of primary versus secondary freshwater fishes. Species representing families of the secondary freshwater fishes Cichlidae and Poeciliidae predominate in nuclear Central America and northwestern LMA (the San Juan, Chiapas-Nicaragua, and Bocas provinces, Fig. 5), whereas primary freshwater fishes are a considerably more prominent feature of southeastern LMA communities. For example, cichlids and poeciliids dominate the freshwater fish community in the San Juan province constituting greater than 60% of the fauna, whereas characids comprise only 18% of the total species richness of the San Juan province and loricariids are completely absent. In contrast, primary freshwater fishes of the Characidae, and to a lesser extent, the Loricariidae, contribute a much larger percentage of the total species richness of the southeastern biogeographic provinces of LMA (the Chiriqui, Santa Maria, Chagres and Tuira provinces, Fig. 5). This is most clearly exemplified by the patterns of community composition in the Chagres province, where characids and loricariids combined make up approximately 50% of the fauna, while poeciliids and cichlids represent only 17% of the total number of species present. Changes in community composition across the lower Mesoamerican landscape are not mirrored by changes in the species richness of the biogeographic provinces. Species richness is highest at the eastern extreme of LMA, but does not decline smoothly as one travels west reflecting the counteracting contribution of cichlid and poeciliid diversification in northwestern 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).

The central roles of historical processes and hypothesized biological differences among freshwater fish families in determining the distribution and diversity of Mesoamerican freshwater fishes are exemplified by the aforementioned geographic variation of the relative contribution of families of secondary and primary freshwater fishes to the species richness of the LMA biogeographic provinces. 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 and Martin 1998, Perdices et al. 2002), and probably secondary freshwater fishes as well (Murphy and Collier 1996, Martin and Bermingham 1998). The geologic evolution of the LMA landscape determined to a large extent the relative colonization success of the colonists. Several periods of geological development appear to be particularly relevant to the colonization of Mesoamerica by freshwater fishes.

In the mid-Miocene, lower Mesoamerica constituted a series of islands with frequent Pacific to Caribbean marine connections, and Central and South America were separated by an ocean barrier of abyssal-bathyal depths (>2000m) in the region of present-day eastern Panama and the Colombian Choco (Coates and Obando 1996). There is no evidence that primary freshwater fishes colonized Mesoamerica during this time, but molecular analyses suggest that heroine cichlids (Martin and Bermingham 1998) and *Rivulus* (Murphy and Collier 1996) might have arrived approximately 18-15 Ma, an estimate based on an mtDNA cytochrome b molecular clock (1-1.2% sequence divergence per Ma, Bermingham et al. 1997b). How they did so is unknown, however our presumption is that colonization was facilitated by some physiological tolerance of sea water. Nevertheless, the phylogenies for heroine cichlids and *Rivulus* suggest that independent colonization events occurred no more than a few times. Prior to the mid-Miocene, the streams and rivers of the LMA landscape were devoid of primary and secondary freshwater fishes; none of the North American primary freshwater fish families successfully colonized Mesoamerica south of Guatemala, and only the salt-tolerant Neararctic gars have managed to colonize as far south as the Great Lakes basin of Nicaragua and Costa Rica (Miller 1966). Consequently, early LMA freshwater fish colonists encountered empty ecological niches, and thus the presence of numerous novel environments accompanied by their divergent selective pressures. Conditions during the mid-Miocene in nuclear Central America fostered an adaptive radiation among the cichlids and poeciliids in order to fill the "ostariophysan vacuum" that existed in Mesoamerica at the time (Myers 1966, Martin and Bermingham 1998).

The continuing uplift of the Panamanian Isthmus, combined with dramatically reduced sea level (Haq et al. 1987) at the close of the Miocene may have resulted in the ephemeral emergence of the Isthmus, perhaps providing the earliest opportunity for the colonization of LMA by primary freshwater fishes (Savin and Douglas 1985, Bermingham and 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 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 the conditions (diversity and distribution of fishes) of the putative source population in northwestern South America. The species richness of characids and loricariids in northwestern Colombia far surpasses the species richness of other families of freshwater fishes (Table 2). These conditions clearly favored colonization and subsequent allopatric diversification of characids, and to a lesser extent loricariids in eastern and central Panama.

The final closure of the Isthmus was completed approximately 3.5-3.1 Ma, serving to establish a permanent connection between northwestern Colombia and eastern

Panama which in turn, permitted the Great American Biotic Interchange across the LMA landbridge (Marshall et al. 1979, Stehli and Webb 1985, Coates et al. 1992, Coates and Obando 1996). Subsequent geological evolution of the LMA landscape resulted in the isolation of certain areas that had important consequences on the dispersal and diversification of the fauna in these regions (Bermingham and Martin 1998). The rise of the Central Cordillera was an important vicariant event which separated the faunas of the Caribbean and Pacific 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 and Martin 1998). Thus, it is likely that owing to geologic processes, only the first colonization event of primary freshwater fishes reached the northern drainage basins of Costa Rica (Bermingham and Martin 1998), which also contributed to the disparity of the relative richness of primary and secondary fishes across lower Mesoamerica.

Dispersal and in situ speciation following initial colonization events of LMA

The relative importance of dispersal and in situ speciation events in shaping patterns of distribution and diversity of LMA freshwater fishes following initial colonization events described herein varies across the spatial extent of LMA. Fifty-eight percent of the LMA ichthyofauna is endemic to lower Mesoamerica, suggesting that in situ speciation has clearly played an important role in shaping patterns of diversity of the LMA freshwater fish fauna. Nonetheless, it is apparent that dispersal is a persistent aspect of the LMA biota. Certainly, much of the heterogeneity in species turnover owes to specific aspects of the geological history of the Isthmus. Differences in the degree of isolation between regions, combined with other abiotic factors, have largely influenced the relative importance of dispersal and in situ speciation events.

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 exceeded those of adjacent provinces along the same slope in 13 out of 18 cases (Table 3). This contrast in faunal turnover probably owes to two general geological mechanisms: 1) river capture; and 2) river anastomosis across low gradient paleo-landscapes. Both of these geological mechanisms certainly have larger impacts on adjacent drainages on the same slope for two principle 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. Patterns of nestedness among freshwater fishes within a drainage basin preclude 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, suggesting, in sum, that cross-cordillera river capture will only rarely cause a faunal exchange 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.

An obvious exception to the general lack of cross-Cordillera faunal exchange regards the biogeographic provinces of San Juan and Chiapas-Nicaragua, marked by the smallest recorded value of species turnover (Table 3). 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 45m in altitude (Coates and Obando 1996). Dispersal of freshwater fishes has obviously not been as strongly impeded between the San Juan and Chiapas-Nicaragua provinces in comparison to other areas in LMA where the Cordillera reaches much higher elevations and represents a more significant barrier to fish dispersal. The nature of the landscape in this region suggests that the San Juan-Chiapas-Nicaragua dispersal corridor most likely continues to present LMA freshwater fishes with a possible cross-Cordillera dispersal route.

The lack of isolation between the San Juan and Chiapas-Nicaragua provinces suggests that dispersal has had a much more prominent influence on patterns of species richness and endemism in this area, particularly in the Chiapas-Nicaragua province. Furthermore, the lack of environmental stability over ecological and evolutionary time has further exasperated the relative importance of dispersal in this area. The drainage basins of the Chiapas-Nicaragua province experience long dry seasons resulting in the drying up of large portions of streams and large fluctuations in the volume of water and the quantity of silt loading in its rivers during this time (Savage 2002). Such events could cause the local extirpation of resident species which are unable to migrate to refugia during periods of prolonged aridity. Furthermore, different lines of geological evidence suggest that marine corridors existed in the Northern Tempisque, San Carlos, and Northern Limon Basins well into the Pliocene (Coates and Obando 1996). The drainage basins of the Chiapas-Nicaragua province would have been subjected to substantial marine incursions during interglacial periods as a result of the low topography of the region. The large amount of disturbance attributable to the marine transgressions and regressions could have resulted in the local extirpation and/or extinction of freshwater fishes in this area, a process that can be evoked to partially explain the low endemicity and species richness of the area.

The Pacific slope of Panama, owing to the large number of shared species between biogeographic provinces, provides one of the clearest examples of facilitated dispersal among rivers along the same slope. Nineteen of the 27 species shared between the Chiriqui and the Santa Maria are also shared with the Tuira province. The somewhat recent development of the Sona peninsula and the coastal mountain chain that now bisects the Santa Maria and Chiriqui provinces suggests that river capture was of more frequent occurrence in the not so distant past, which would have permitted faunal exchanges between the Chiriqui and Santa Maria provinces. In contrast, subsequent to the development of the Sona peninsula, the likelihood of river capture and ensuing dispersal events between the provinces would have probably decreased. Indeed, fishes from the third LMA colonization event (2-0 Ma) were unable to disperse from the Santa Maria province to the Chiriqui province (Bermingham and Martin 1998).

Nevertheless, thirty percent of the Chiriqui fauna is endemic to the province (Fig. 7), suggesting that in situ speciation also played an important role in shaping present-day patterns of distribution and diversity in the Chiriqui province. The extremely high rainfall (4 000-6 000mm) combined with the shortened dry season that occurs in the Rio Terraba and Rio Coto present the freshwater fishes of this region with a less variable environment which might be responsible for reduced cases of local extirpation/extinction events in the Chiriqui province (Savage 2002). Moreover, our measure of beta diversity (Table 3) indicates that the Cordillera Costena, which extends to the Pacific just north of Punta Mala is relatively impermeable to the dispersal of freshwater fishes, further contributing to the isolation of the Chiriqui province, a factor that has certainly influenced the high degree of endemism observed in this region.

Dispersal events resulting from river anastomosis occurring during periods of reduced sea level clearly have had a large impact on the faunal similarity of the Santa Maria and Tuira provinces. Thirty-one species are shared by the Santa Maria and Tuira provinces and the faunal turnover between these provinces is relatively low (Table 3). 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 and Martin 1998). Combined with periods of reduced sea-level during glacial maxima, the gradual decline of the continental shelf of the Bay of Panama would have greatly facilitated fish dispersal through anastomizing lowland streams and swamps ranging from the Rio Tuira to the streams of the Azuero Peninsula (Loftin 1965, Bermingham and Martin 1998). Our GIS modeling analysis (Fig. 8) 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 to present the paleodrainage patterns with precision. Historical processes facilitating dispersal between drainages in this area have had a large influence on patterns of distribution and diversity observed in the Santa Maria and Tuira provinces.

The pan-Pacific dispersal corridor of central Panama is contrasted by the relative isolation of Bocas province from adjacent provinces on the same slope (Table 3). In situ speciation has clearly had a large impact on patterns of distribution and diversity in this region; 39% of the fauna is endemic to the province (Fig. 7). Our analyses indicate that very strong dispersal barriers exist between the San Juan and Bocas provinces, as well as between the Chagres and Bocas provinces. The fauna of the Bocas province may have been derived from an initial colonization event 7-4 Ma, followed by subsequent isolation of the province from the rest of LMA approximately 3 MA (Bermingham and Martin 1998). The relative degree of isolation of the Bocas province from its Caribbean slope neighbors can be partly attributable to the steep incline of the continental shelf in this area. Drainage anastomosis during periods of lowered sea level may be less frequent in this area than in central Pacific Panama owing to differences in the incline of the continental slope in these two areas.

Distribution of species ranges and dispersal limitation

The simplest manner in which to express a geographic range is by the number of sites occupied by a species in a given region, such that the distribution of species ranges may be expressed as a function of the number of biogeographic provinces occupied (Fig. 9). The distribution of range size for the freshwater fishes of LMA is geometric, whereby many more species have small ranges than have 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). Similarly, Hugueny (1990) reported a geometric distribution for the range size of Nilo-Sudanian freshwater fishes. Gaston (1994, 1996) has argued that the mechanisms responsible for patterns of range size distribution such as we have observed are a consequence of 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 where the demographic properties of individuals are the same and dispersal gives rise to many of the macroecological patterns reported in the literature (Bell 2001, Hubbell 2001). Dispersal limitation, whether it is as a manifestation of neutral processes, or a function of the distribution of habitat across the landscape, or some combination thereof, is likely responsible for the patterns of range size distribution observed.

Hubbell (2001) examined communities of mixed medophytic forest, marine plankton copepods, the Barro Colorado Island bat community, andrenid bee community (Utah), insectivorous birds of Hubbard Brook (New Hampshire), British breeding birds and the Cano Maraca fish community in Venezuela, and found that the latter exhibited the greatest dispersal limitation of all of the examined communities. Using the Unified

Neutral Theory of Biodiversity and Biogeography, Hubbell (2001) estimated an immigration parameter of only one in 10,000 births (or m=0.0001) for this headwater fish community. Many of the examined communities did not display any dispersal limitation, and the next most dispersal limited community examined by Hubbell (2001) was that of the insectivorous birds, which had an estimated immigration parameter of 0.2, underlining the degree of dispersal limitation of freshwater fish communities. Perhaps Myers (1938) best described the dispersal potential of freshwater fishes in the following passage: "Throughout the world the migrations of freshwater fishes over extensive continental areas have generally been excessively slower than those of almost any creature that can creep, crawl, walk, or fly, however closely that creature may have been bounded by its ecological tolerances." The dispersal limitation of freshwater fishes (Hugueny 1990, Hubbell 2001, present study) relative to other organisms suggests that historical processes may play a more important role in the patterns of distribution and diversity among freshwater fishes than other organisms.

If colonization from one drainage basin to another resulting from dispersal along the coastline is frequent, the hypothesized salinity tolerance of secondary freshwater fishes should confer a dispersal advantage on these fishes, and thus, secondary freshwater fishes should have larger geographic ranges. 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 biogeographic provinces (Fig. 9). There is no significant difference between the average range size of the primary and secondary freshwater fishes of LMA (two tailed t-test, p=0.368). Therefore, the differential salinity tolerance that distinguishes primary freshwater fishes from secondary freshwater fishes is not an important determinant of range size and thus, the dispersal of secondary freshwater fishes along coastlines must be a fairly infrequent event. 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 islands, which geologic evidence suggests have been connected to continental land masses during the Cenozoic, whereas the distribution of secondary freshwater fishes includes many islands that did not experience continental connections in the Cenozoic (West Indian islands, Madagascar, the Seychelles, etc., Myers 1949). The distributional patterns of these fishes suggest that although secondary freshwater fishes are not normally found in saline conditions, narrow sea barriers may be crossed (Myers 1949). Nevertheless, the potential dispersal advantage conferred on secondary freshwater fishes must be mitigated by the infrequent nature of dispersal events along the coast. This finding is consistent with Myers' (1949) hypothesis that primary and secondary freshwater fishes usually employ similar methods of dispersal. The hypothesis that secondary freshwater fishes may be able to cross sea barriers, but do so very infrequently, would explain how the differential ability to tolerate changes in salinity has not conferred a short-term dispersal advantage on secondary freshwater fishes, while reconciling how the ability to tolerate changes in salinity enabled a small number of these fishes to colonize LMA approximately 10 Ma prior to the initial colonization of LMA by primary freshwater fishes.

CONCLUSION

Patterns of the distribution and diversity of lower Mesoamerican freshwater fishes demonstrate the penetrating and long-lasting effects of regional and historical processes on biological communities. Our results, viewed in light of the hypotheses proposed in Bermingham and Martin (1998) and Martin and Bermingham (1998), indicate how the geologic development of the Panamanian Isthmus has influenced the evolution of the lower Mesoamerican freshwater fish fauna. The filtering effect of LMA biogeographic barriers has changed in space (distance from source populations) and over time. Colonization events from South America have met increasing resistance as a result of the geologic evolution of the LMA landscape, giving rise to the patterns reported herein. Another plausible explanation for differential temporal colonization success is that increasing species richness acted to retard the expansion of later arriving species. Local communities of freshwater fishes in the drainage basins of the Panama Canal, however, were not resistant to invasion, nor were they vulnerable to extinction following invasion, suggesting that geological rather than local deterministic processes are more important in determining the dispersal success of colonists participating in different colonization events (Smith et al. submitted).

Diversity anomalies in matched communities in different regions provide one of the best lines of evidence that history imparts a powerful imprint on the composition and species richness of local communities. Comparison of diversity anomalies between communities of freshwater fishes in eastern Panama and northern Costa Rica suggests that differential patterns of community composition and species richness arise as a result of the unique historical circumstances that surrounded the colonization of LMA. The combined influence of historical processes and intrinsic biological differences between freshwater fish families appears to have permitted secondary freshwater fishes to colonize Mesoamerica approximately 10 Ma prior to primary freshwater fishes, giving rise to the disparity of community composition observed across lower Mesoamerica. It is important to note, however, that hypothesized biological differences between primary and secondary freshwater fish families have not given rise to differences in the average geographic range sizes between families of primary and secondary freshwater fishes, suggesting that dispersal events of secondary freshwater fishes along coastlines must be infrequent. Even so, the turnover in community composition across lower Mesoamerica clearly highlights the importance of biological differences among species to patterns of distribution and diversity of organisms observed at the continental scale, providing clear evidence of non-neutral patterns at large spatial scales.

History has left an important imprint on the freshwater fish fauna of LMA, owing to the recent colonization of LMA by freshwater fishes as well as the dispersal limitation of strictly freshwater organisms. Our results permit the inference that history has a primary influence on the distribution and diversity of biological communities, and that the ecological interactions among species are not independent of a region's history. The interactions among species in any given community are defined by the historical events responsible for the assembly of that fauna. Thus, our study permits the inference that regional and historical processes probably play an ongoing role in the maintenance of LMA freshwater communities. Furthermore, our results suggest that processes responsible for the assembly and maintenance of biological communities at the local scale cannot be understood without first understanding the regional and historical processes of the region, which lends support to the importance of a top-down approach to the study of species richness and diversity (Tonn et al. 1990, Ricklefs and Schluter 1993, Whittaker et al. 2001).

ACKNOWLEDGEMENTS

We would especially like to thank Gustavo A. Concheiro P. for his help with GRASS and GIS related analyses presented in this manuscript. We would also like to thank the following people, who provided invaluable assistance in the preparation of the data presented herein: Vijay Aswani, Grettehun Grajales, Rigoberto Gonzalez, Oris Sanjur as well as other members of the Bell and Bermingham labs for their support. Bernard Hugueny provided insightful statistical advice as well as commented on a previous draft of this manuscript. SAS was supported entirely by the Canadian government through a Natural Sciences and Engineering Research Council of Canada PGS A scholarship. We would also like to thank the Smithsonian Tropical Research Institute for financial and logistical support.

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Table 1: Results from two separate partial Mantel's tests that were used to evaluate the significance of the faunistic relationships among 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's tests that were performed. Each partial Mantel's 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	r	# of permutations	P Value
Euclidean distance	0.447	9 999	$p<0.0005$
Jaccard's similarity coefficient	0.609	9 999	$p<0.0005$

Table 2: Contribution of several freshwater fish families to the overall species richness of the Rio Atrato and Rio Magdalena drainage basins in northwestern Colombia.

Freshwater Fish Family	Physiological Division	Percent 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%

Table 3: Specific covariation among the biogeographic provinces of LMA. A larger specific covariation indicates lower beta-diversity (or lower species turnover between biogeogrpahic provinces).

	San Juan	Chiapas-Nicaragua	Bocas	Chiriqui	Santa Maria	Chagres	Tuira
San Juan	X						
Chiapas-Nicaragua	0.087	X					
Bocas	0.028		X				
Chiriqui	-0.031	0.020	-0.011	X			
Santa Maria			-0.002	0.073	X		
Chagres			-0.007		0.053	X	
Tuira					0.063	0.071	X

Figure 1: Drainage basins of lower Mesoamerica.

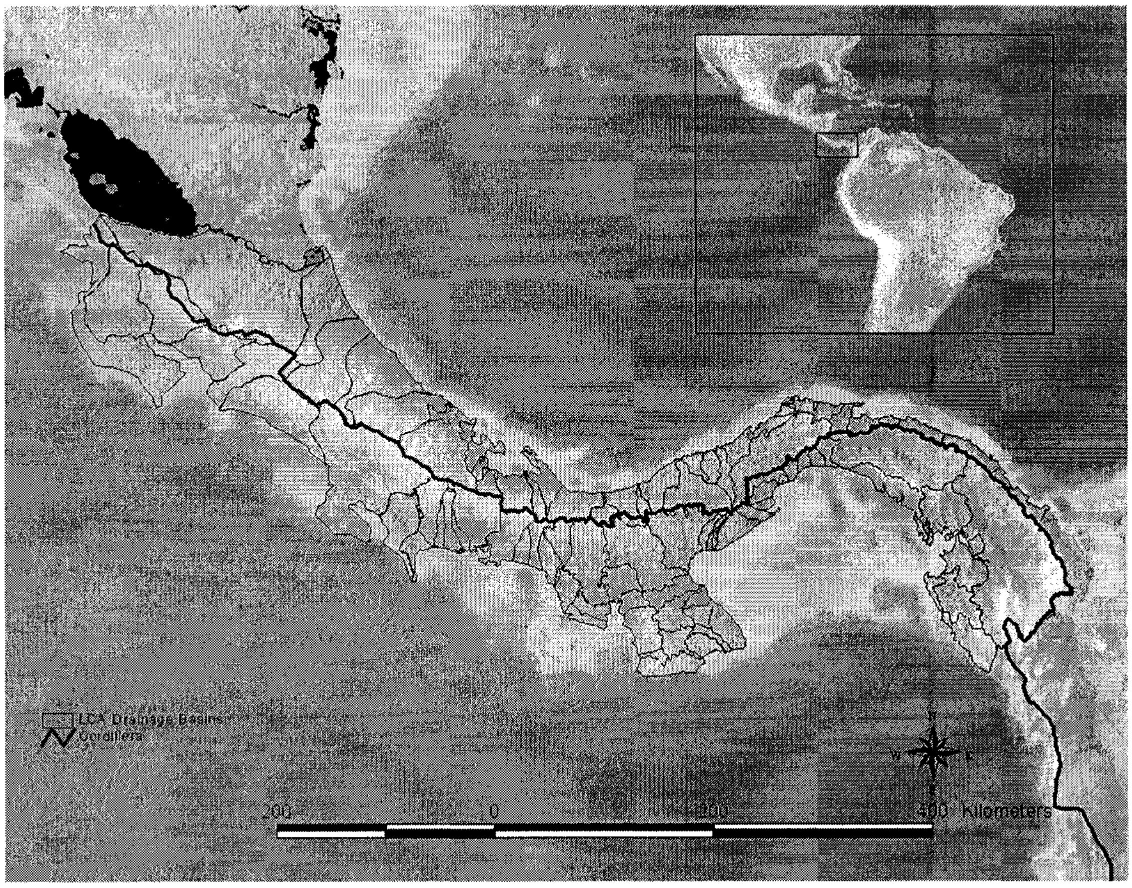


Figure 2: The biogeographic provinces of LMA. The faunistic relationships between LCA drainage basins were inferred based on concordance between methodologies and summarized to describe the biogeographic provinces of LMA freshwater fishes depicted in this figure.

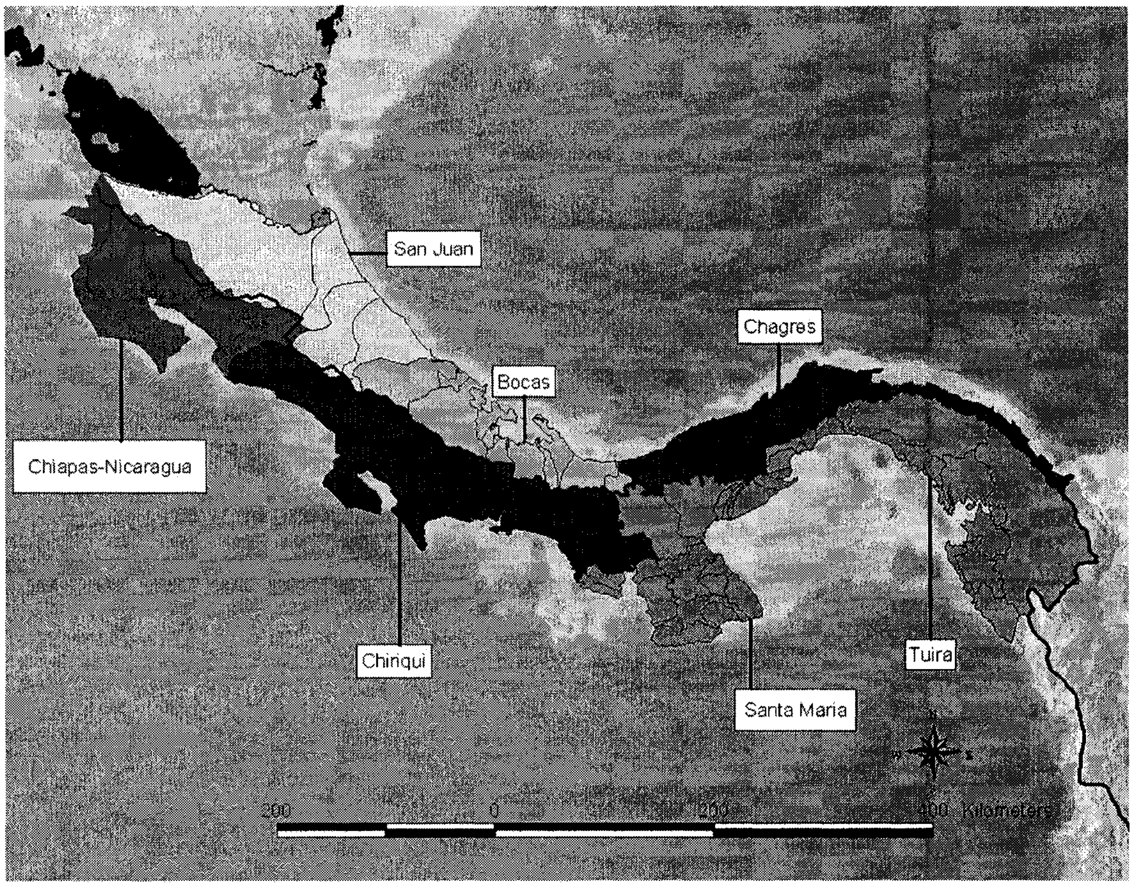


Figure 3: Dendogram depicting the faunal relationships among LMA drainage basins as defined by a UPGMA cluster analysis based on the measure of Euclidean distances.

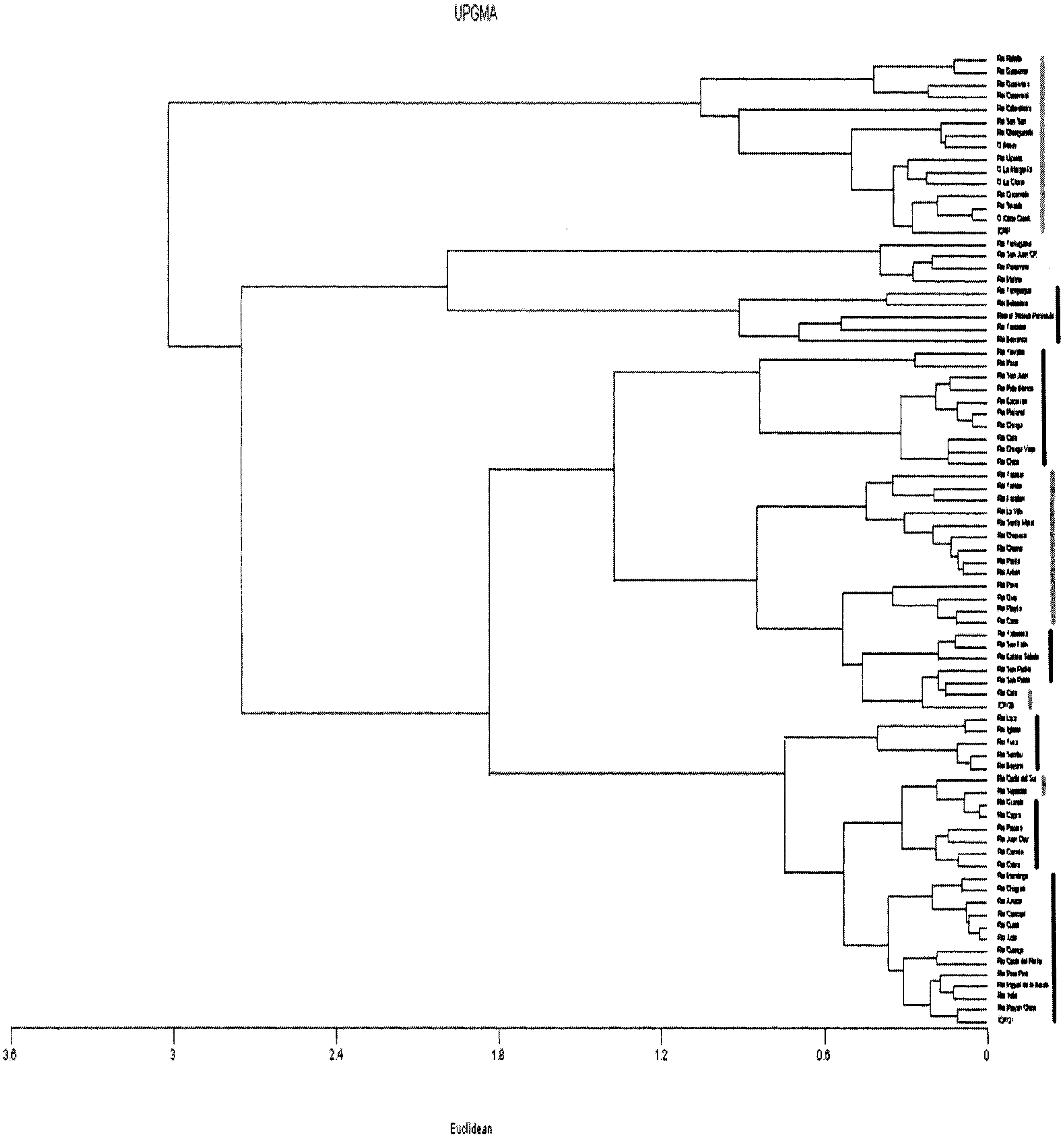


Figure 4: Dendogram depicting the faunal relationships among LMA drainage basins as defined by a UPGMA cluster analysis based on Jaccard's similarity coefficient.

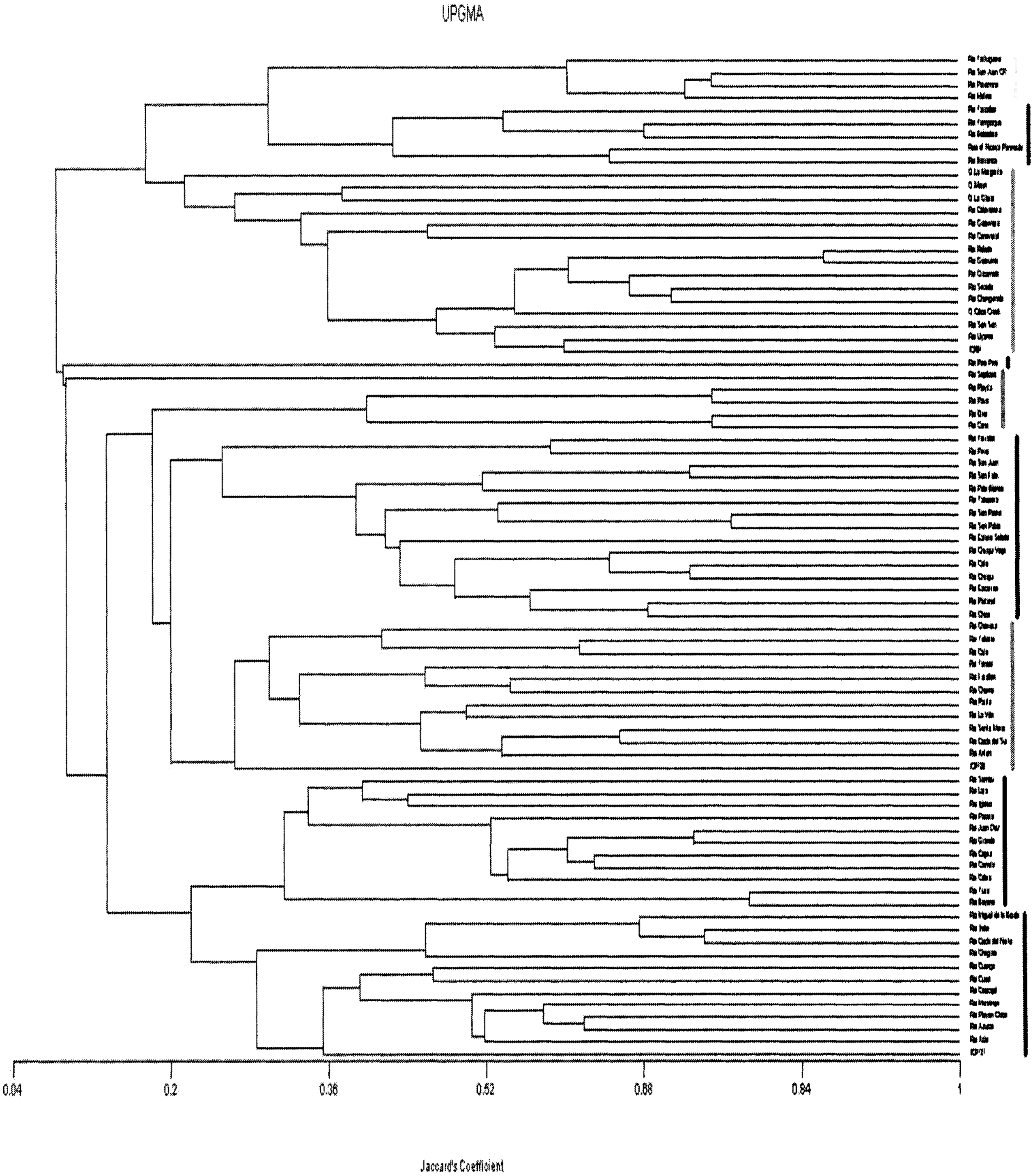


Figure 5: The relative contributions of selected families of LMA freshwater fishes to the species richness of the LMA biogeographic provinces.

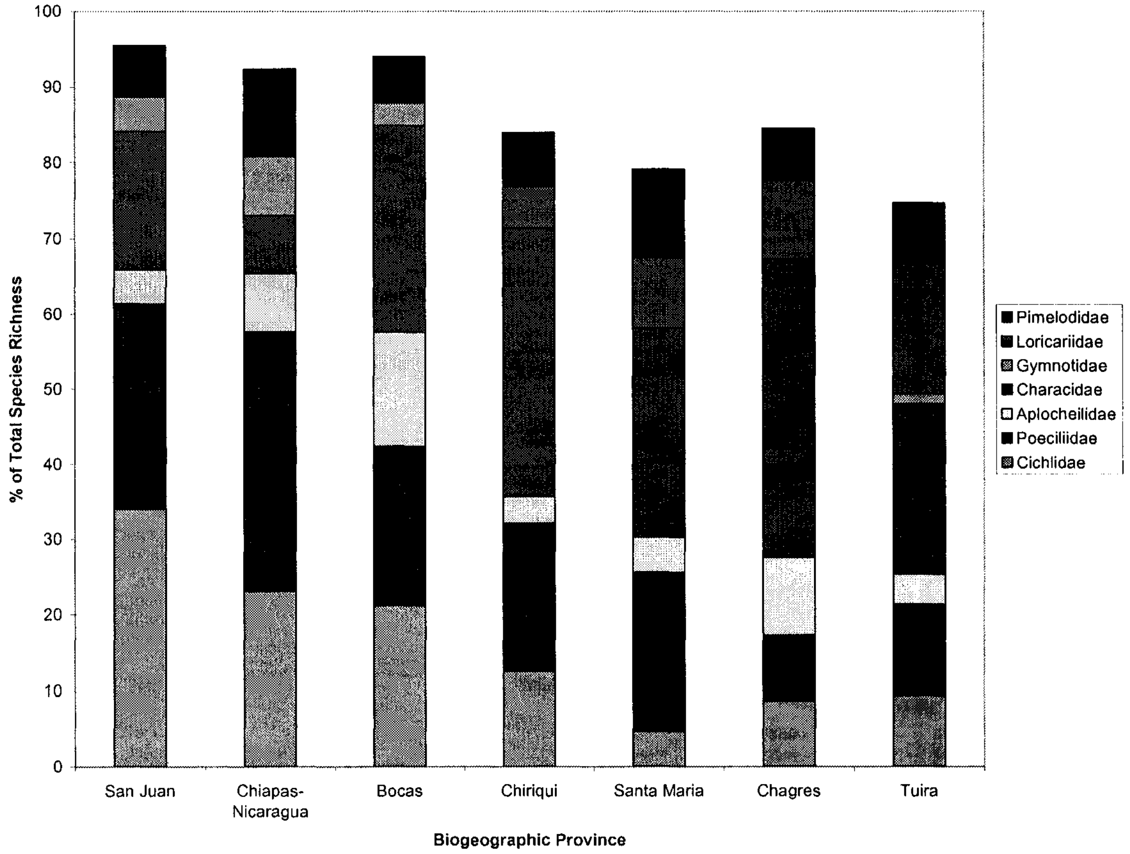


Figure 6: Species richness of the biogeographic provinces of LMA.

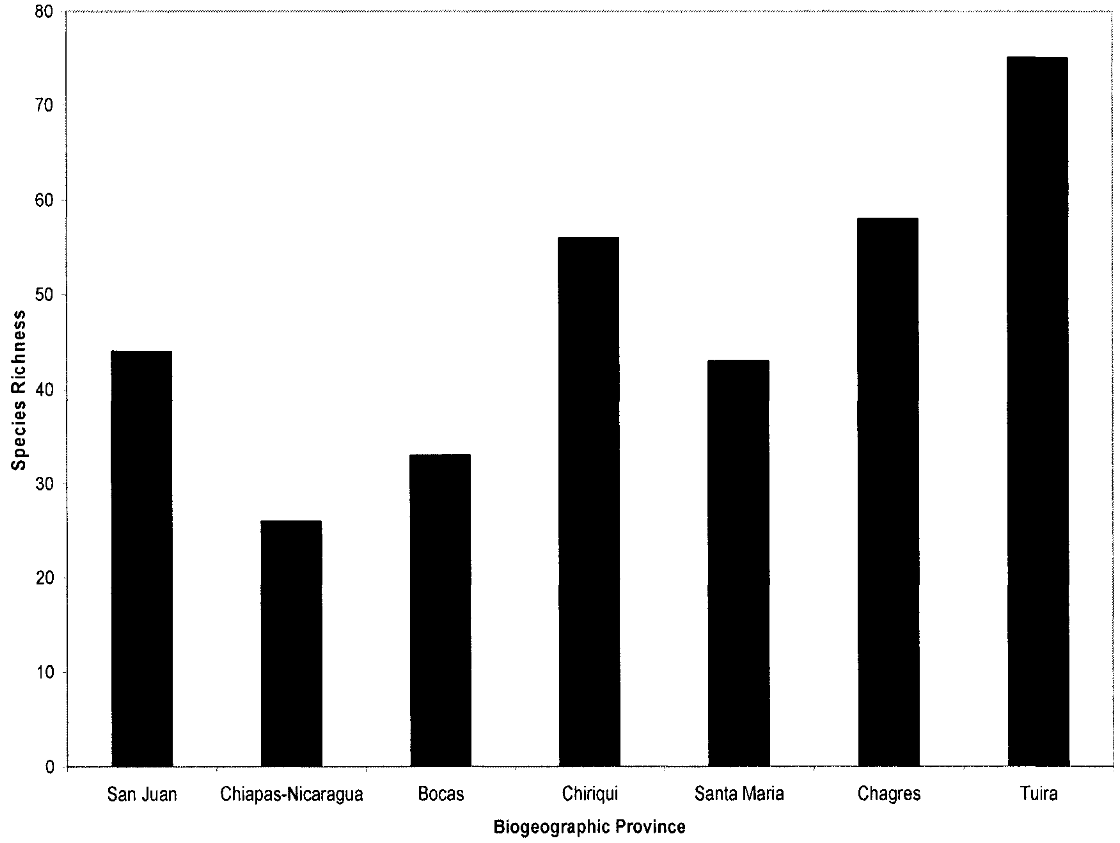


Figure 7: Endemicity of each LMA biogeographic provinces. We defined endemism as species that are endemic to LMA and whose ranges are limited to one biogeographic province.

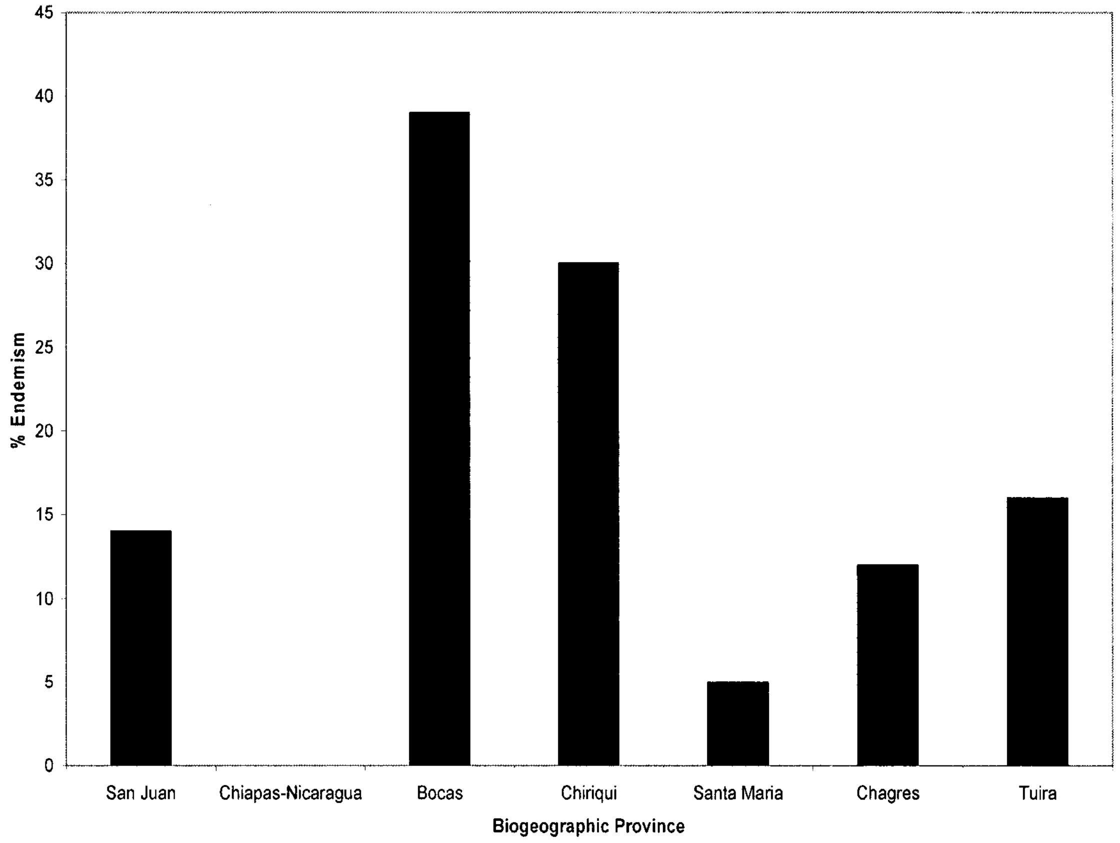


Figure 8: Bathymetric streams of LMA during the last interglacial (sea level was set at -110m from present sea level). The bathymetric streams were modeled using the r. function of GRASS.

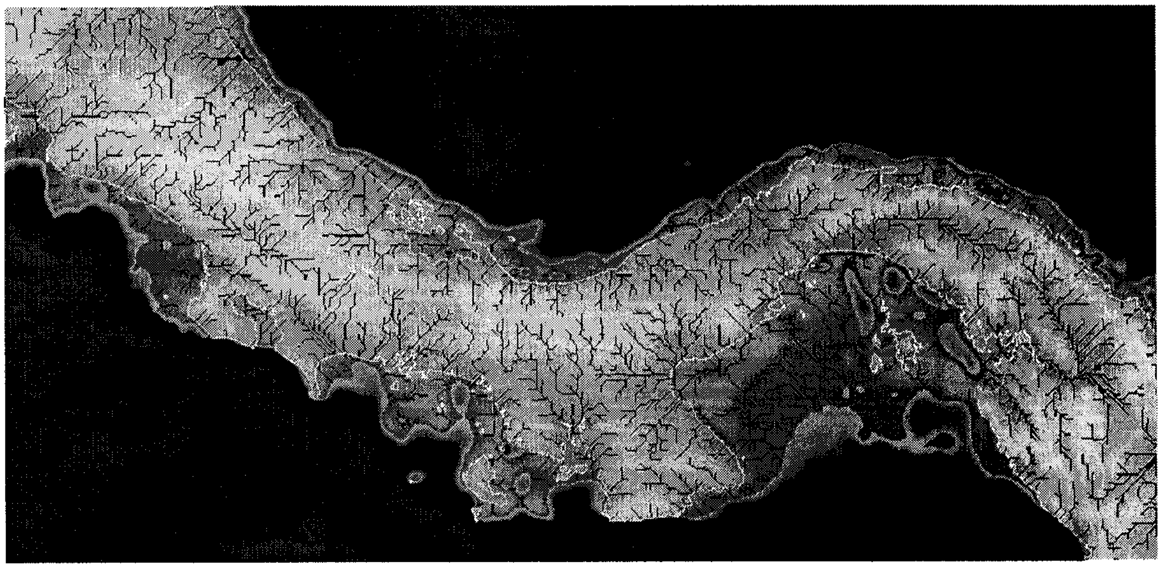
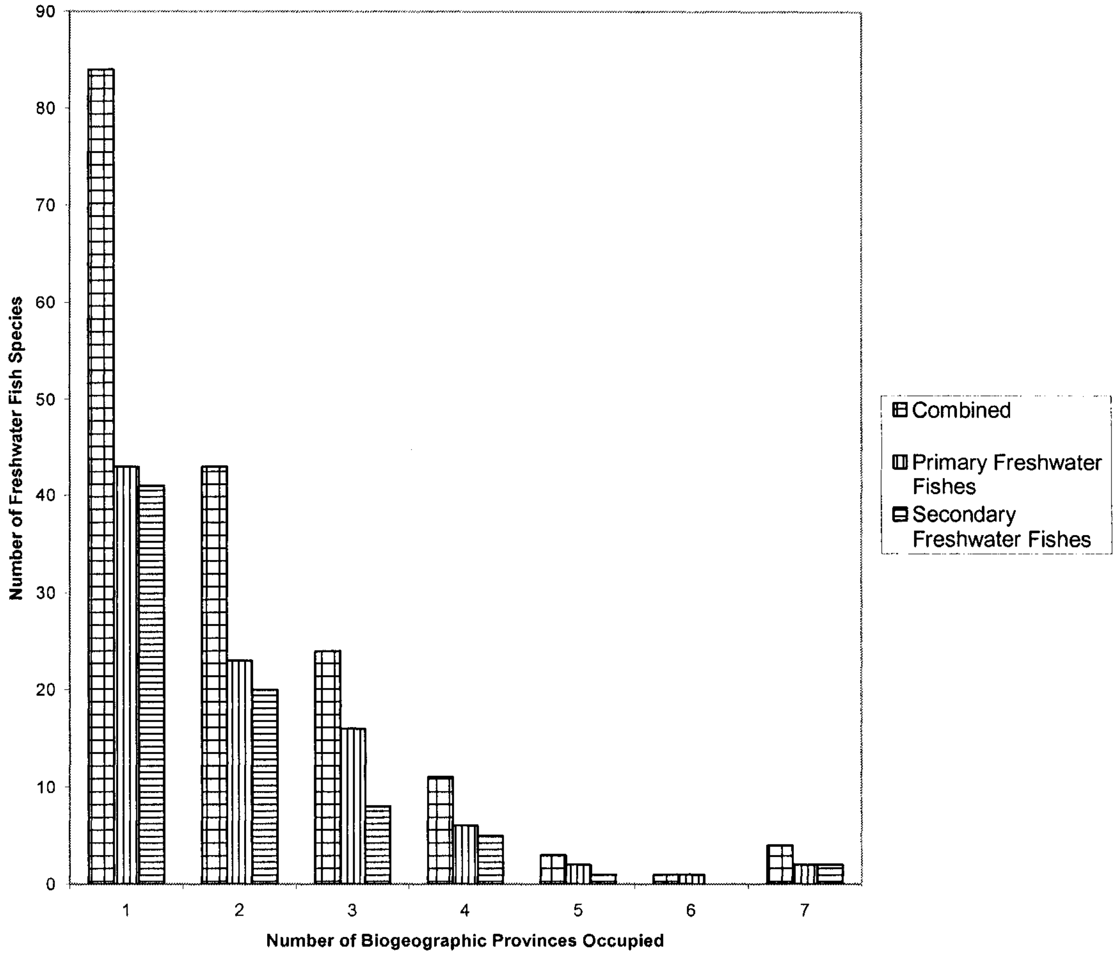


Figure 9: The distribution of range size (as measured by the number of biogeographic provinces occupied) for the freshwater fishes of LMA.



Chapter #2: Cross-Cordillera exchange mediated by the Panama Canal increases the species richness of local freshwater fish communities

Cross-Cordillera exchange mediated by the Panama Canal increases the species richness of local freshwater fish communities

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Completion of the Panama Canal in 1914 breached the continental divide and set into motion a natural experiment of unprecedented magnitude by bringing into contact previously isolated freshwater fish communities. The construction of a freshwater corridor connecting evolutionarily isolated communities in Pacific and Caribbean watersheds dramatically increased the rate of dispersal, without affecting other environmental variables. Here, we report that a large fraction of species have been able to establish themselves on the other side of the continental divide, whereas none have become extinct, leading to a local increase in species richness. This demonstrates that community composition and species richness were regulated by the regional process of dispersal, rather than by local processes such as competition and predation and that local communities were not saturated.

Patterns in natural communities have often been studied to understand the ecological mechanisms underlying them. One extreme view is that communities are closely fitted to the landscapes they inhabit, each species occupying a distinctive niche and contributing an essential element to overall community function. The extinction of any species is likely to impair community processes, and invasion is unlikely, because communities are already “saturated” with well-adapted species. However, if invasion occurs it will be disruptive and is likely to cause the extinction of one or more resident species. The opposite view is that communities are loosely organized, with most species not precisely adapted to the sites they occupy. Extinction of a species will seldom have any substantial effect at the community level, and invasion is commonplace but will not necessarily, or often, cause the extinction of resident species. Two manifestations of these opposed points of view are the clash between neutralist and functionalist interpretations of community properties, and the debate concerning local and regional effects on species richness. Relationships such as those between species richness and area, distribution and abundance, or local and regional richness have been extensively analyzed in an attempt to understand the mechanisms that give rise to them (1-8). The best-known and best-documented ecological patterns are readily explained, however, either by simple neutral models in which all individuals are ecologically identical or by more complex models involving specialization and niche partitioning (9, 10). Natural experiments, where the dynamic balance between local and regional processes is disturbed, and the change in local species richness over time is documented (11, 12), provide a more powerful means for evaluating the relative importance of deterministic, local, selection-driven processes and stochastic, regional, dispersal-driven processes in shaping the attributes of natural communities. Suitable natural experiments have not yet been reported in the literature.

Completion of the Panama Canal in 1914 created a freshwater corridor between the Rio Chagres on the Caribbean slope of the Isthmus of Panama and the Rio Grande on the Pacific slope, enabling the freshwater fish communities occupying the hitherto isolated drainage basins to intermingle. Although the Central American continental divide is relatively low in the region of the Panama Canal, it was nonetheless an effective barrier to the dispersal of freshwater fishes before the construction of the Panama Canal (13). The breaching of this barrier allowed increased fish dispersal between drainages, without directly altering environmental conditions or species interactions. Thus, the natural experiment initiated with the flooding of the Panama Canal offers a rare opportunity to test whether dispersal-driven or selection-driven processes governed the attributes of fish communities in the rivers of the Panama Canal watershed.

S.E. Meek and S.F. Hildebrand, ichthyologists associated with the Smithsonian Biological Survey of the Panama Canal Zone, conducted a survey of the freshwater fishes in the Rio Grande and Rio Chagres between January 1911 and March 1912 (13). These collections, completed before the breach of the continental divide, provide the historical baseline for the comparison of changes in the species richness of the primary and secondary freshwater fish communities of the Rio Chagres and the Rio Grande. In order to standardize our experiment to the historical baseline, we considered only those species determined to inhabit the Rio Chagres and the Rio Grande by Meek and Hildebrand (13) and Hildebrand (14, Table 1) . Our contemporary survey of fishes from the rivers and streams draining into the Panama Canal watershed (15, see supplemental information) enabled us to document cross-continental divide colonization events, and determine whether or not local extirpation had occurred in the freshwater communities of the Rio Grande and the Rio Chagres. Comparisons between our survey of the freshwater fishes of the Panama Canal Watershed and that of Meek and Hildebrand's (13) attest to the efficiency of their description of the freshwater fish fauna of the Rio Chagres and the Rio Grande (see Table S1).

Many species were able to disperse through the Canal and establish themselves on the other side of the divide (Fig. 1). We documented 3 species of freshwater fishes that colonized the Rio Chagres from the Rio Grande and 5 species of freshwater fishes colonizing the Rio Grande from the Rio Chagres (Table 1). The colonists represented 75% and 38.5% of the total number of species that were potentially able to colonize the Rio Chagres from the Rio Grande (and vice versa) and which had not already done so prior to the construction of the Panama Canal. If, however, we adopt a less conservative approach and consider the community of freshwater fishes not limited to those species initially collected by Meek and Hildebrand (13), but whose geographic range (15) suggests that they might represent post-Canal additions to the Rio Chagres and the Rio Grande, we document the addition of 2 further species of freshwater fishes in the Rio Chagres (*Imparales panamensis* and *Vieja tuyrensis*) and 1 additional species in the Rio Grande (*Brycon obscurus*, see Table S1). In subsequent analyses presented herein, we will only consider our conservative estimate of cross-Cordillera colonists. Nevertheless, in either scenario the surprisingly large percentage of species from the regional pool that was able to invade communities on the other side of the divide shows that in general, resident species were not specifically adapted to pre-existing environmental conditions.

Furthermore, our results suggest that no species have been locally extirpated as a consequence of the cross-divide movement of freshwater fishes through the Panama Canal. Consequently, net species richness increased by 10% in the Rio Chagres, and by 22% in the Rio Grande. This shows that these communities were not ecologically saturated and had not reached any upper limit to number of species that could be supported by the ecosystems before the flooding of the Panama Canal.

A possible objection to these conclusions is that the colonizing species are established only as rare migrants that play no appreciable part in community dynamics. We can evaluate the quantitative success of colonization by counting the number of sites occupied by colonists and the relative abundance that colonists achieve within the local communities (16). One of the 6 freshwater fish colonists for which we have quantitative information was more successful in its translocated range than in its native range in terms of both the relative abundance achieved and the number of sites occupied (Fig. 2A, B). Moreover, several of the other colonists attained similar quantitative success in both drainage basins (Fig. 2A, B). Nested ANOVA analyses of species log transformed abundances in adjacent watersheds indicate that *Cyphocharax magdalenae* was significantly more abundant in its translocated drainage basin, whereas *Roeboides occidentalis*, *Ancistrus chagrensis* and *Roeboides guatemalensis* (data not presented in Fig. 2B) were significantly more abundant in their native versus their translocated drainage basin. For all other species reported in Fig. 2B, there was no statistically significant difference between abundance in native and translocated drainages (Table 2). In many cases, therefore, the invading species achieve a level of distribution and abundance comparable with or even greater than that in their source communities.

It is conceivable that the translocated populations, although large, might be maintained primarily through dispersal from the source populations and do not constitute truly autonomous self-sustaining invasions. Current evidence indicates that this is unlikely. Previous studies of the freshwater fishes of the Panama Canal have documented the extensive use of shoreline habitat in Lake Gatun (created as a result of the flooding of the Panama Canal) by riverine species, facilitating dispersal between opposite slope drainage basins (17). *Cichla ocellaris*, a predatory fish of South American origin, devastated the Lake Gatun shoreline community after its introduction in 1967, and populations of cross-divide colonists such as *Astyanax* and *Roeboides* were almost completely extirpated (17). The Lake Gatun population of *Cichla ocellaris* has acted for thirty-six years as a barrier to the dispersal of fish through the Panama Canal, making it unlikely that metapopulation source-sink dynamics could explain the maintenance of the populations of cross-divide colonists in their translocated drainage basins.

It is also conceivable that the invasion of an exotic species is followed by the extinction of a resident species only after a considerable period of time, so that local extirpation events have not yet occurred because the Panama Canal experiment has not yet had enough time to play itself out. However, if competitive exclusion is an important process setting limits on the species richness of local communities, our results suggest that it does not occur on the time scale of 10 to 100 generations that is usually envisaged (18). We have documented no cases of local extirpation across the 89 years of the Panama Canal experiment. Our observations are consistent with paleontological studies of biotic interchanges, which indicate that species invasions following the elimination of a dispersal barrier rarely cause the extirpation of residents on evolutionary time scales (19-21).

Finally, local and regional processes might act over completely different time scales (3, 18), so that the lack of saturation that we have recorded for freshwater fish communities of the Panama Canal could be a result of the relatively young age of the lower Central American freshwater fish fauna, particularly the primary fish fauna which colonized this region in the early Pliocene (22). It is possible that there has not been sufficient time for the process of speciation to 'saturate' local communities with species, and this would enhance the importance of dispersal, relative to local deterministic processes, in governing the number of species coexisting in local communities. In that case, it would not be possible to evaluate rival ecological mechanisms in communities that have existed for less than 5 million years. Phylogeographic analyses of *Anolis* lizards on Caribbean islands, however, demonstrate that after 30 million years of adaptive radiation the species richness of local communities is still increasing and remains below the speciation-extinction equilibrium (23). Speciation may be so slow that few communities ever approach evolutionary equilibrium (23, 24).

We have not been able to identify any characters that differ consistently between species that did and did not succeed in crossing the divide. For example, both trophic generalists (*Brycon chagrensis*, *Astyanax aeneus*) and trophic specialists (*Roeboides occidentalis* and *Roeboides guatemalensis*) successfully participated in cross-divide colonization events (see Table S2). In addition, Vermeij (25) and Ricklefs and Schluter (11) predicted that faunal exchanges should be asymmetrical, with invaders from the more species-rich region having the greater colonization success because they have evolved superior defenses against predators and diseases (26-29). We have identified similar numbers of successful invaders in each direction, however, in spite of the fact that the pre-Canal Chagres basin contained 33% more species that the Rio Grande.

Furthermore, our quantitative assessment of species' colonization success does not indicate that colonists from the more species-rich Rio Chagres were able to achieve greater occupancy success or higher relative abundances in their translocated drainage basins than colonists from the Rio Grande (Fig. 2 A, B). The hypothesis that species from species-rich regions are superior competitors is not supported by our results.

The outcome of biological invasions can in principle be used to evaluate the degree of saturation of local communities (30-32). In practice, most examples reported in the literature are difficult to interpret in these terms. Many have been undertaken at spatial scales that are too large to determine the relative importance of local processes (30, 32-36). Moreover, studies at large spatial scales combine both native and humanized landscapes (30, 32-33), which is inappropriate because invasive species often preferentially occupy humanized landscapes whereas native species have a greater affinity for native, undisturbed habitat (32-33, 37-41). Further complicating comparisons is the hypothesis that disturbed habitat may not be able to support the same number of species as undisturbed habitat (33). Several studies also document extinctions that either occurred prior to the introduction of exotics to the region/locality in question or were the result of the introduction of nonvolant top predators (32, 42), or the destruction of native habitat (33, 37). We have not been able to find any case that documents the results of a biotic interchange following the fusion of two modern, previously isolated local communities. Unlike biotic interchanges, many biological invasions occur following human-driven introductions, and thus ignore the importance of dispersal per se. Studies that compare the reciprocal effects of increased likelihood of dispersal between local communities permit a more stringent test of ecological theory (see 24) and a novel contribution to our understanding of the processes responsible for observed patterns of biological diversity.

Species invasions mediated by human activity are commonplace (30, 43-47), but while particular examples have been studied intensively it has seldom been possible to quantitatively evaluate the outcome of the fusion of two comparable communities. The opening of the Panama Canal has provided an unusually convincing test of ecological theory by connecting two adjacent but independently evolved communities of freshwater fish. The results clearly contradict the view that the fish communities of this region were saturated with species specifically adapted to local conditions. The communities were not resistant to invasion, nor were they vulnerable to extinction following invasion. Rather the results are consistent with the predominance of regional effects, in which ecological differences between species are largely over-ridden by immigration, and are even consistent with strictly neutral community models in which no such differences exist. The value of this large-scale unintentional experiment is that it provides, for this situation, a clear answer to a question that has long been inconclusively debated. Similar experiments are likely to provide us with the most convincing analysis of ecological mechanisms.

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Acknowledgements

We would like to thank Luis Fernando De Leon, Rigoberto Gonzalez, Neilan Kuntz, Andrew Moeser, Gisela Reina and Oris Sanjur for their help in the field. S.A.S. was supported by a Natural Science and Engineering Research Council PGS A scholarship. We thank the Smithsonian Tropical Research Institute for financial and logistical support. The Autoridad Nacional del Medio Ambiente (ANAM) and the Autoridad de la Region Interoceanica (ARI) in Panama kindly provided the required sampling and access permits.

Tables and Figures

Table 1: The primary and secondary freshwater fish communities of the Rio Grande and Rio Chagres drainage basins sampled by both Meek and Hildebrand (13) and the present study. In order to standardize our analyses to the historical baseline provided by Meek and Hildebrand (13), we only considered species collected in their survey of the freshwater fishes of the Panama Canal watershed. Colonists and the direction of colonization are indicated by the arrows depicted in the Direction of Migration column. **Cyphocharax magdalenae* was not captured by Meek and Hildebrand (13), however, the authors captured it in the drainage basins adjacent to the Rio Grande and concluded that it was indeed part of the pre-1914 fauna of the Rio Grande. In addition, the geographic distribution of *Cyphocharax magdalenae* suggests that this species migrated through the Panama Canal. ** *Brachyhypopomus occidentalis* was not captured in the Rio Grande by Meek and Hildebrand (13), probably owing to both its rarity and the difficulties involved in collecting this fish, and consequently we have not considered this species as a cross-divide colonist.

Pre-1914 Rio Grande	***Present-Rio Grande***	***Direction of Migration***	***Present-Rio Chagres***	***Pre-1914 Rio Chagres***
Astyanax aeneus	Astyanax aeneus	→	Astyanax aeneus	
Astyanax ruberrimus	Astyanax ruberrimus		Astyanax ruberrimus	Astyanax ruberrimus
	Brycon chagrensis	←	Brycon chagrensis	Brycon chagrensis
	Brycon petrosus	←	Brycon petrosus	Brycon petrosus
Bryconamericus emperador	Bryconamericus emperador		Bryconamericus emperador	Bryconamericus emperador
Compsura gorgonae	Compsura gorgonae		Compsura gorgonae	Compsura gorgonae
Gephyrocharax atricaudata	Gephyrocharax atricaudata		Gephyrocharax atricaudata	Gephyrocharax atricaudata
			Hyphessobrycon panamensis	Hyphessobrycon panamensis
			Pseudocheirodon affinis	Pseudocheirodon affinis
Roeboides occidentalis	Roeboides occidentalis	→	Roeboides occidentalis	
	Roeboides guatemalensis	←	Roeboides guatemalensis	Roeboides guatemalensis
Cyphocharax magdalenae*	Cyphocharax magdalenae	→	Cyphocharax magdalenae	
Hoplias microlepis	Hoplias microlepis		Hoplias microlepis	Hoplias microlepis
Piabucina panamensis	Piabucina panamensis		Piabucina panamensis	Piabucina panamensis
	Ancistrus chagrensis	←	Ancistrus chagrensis	Ancistrus chagrensis
			Chaetostoma fischeri	Chaetostoma fischeri
Hypostomus panamensis	Hypostomus panamensis		Hypostomus panamensis	Hypostomus panamensis
			Rineloricaria uracantha	Rineloricaria uracantha
Pimelodella chagresi	Pimelodella chagresi		Pimelodella chagresi	Pimelodella chagresi
Rhamdia quelen	Rhamdia quelen		Rhamdia quelen	Rhamdia quelen
	Brachyhypopomus occidentalis**		Brachyhypopomus occidentalis	Brachyhypopomus occidentalis
Aequidens coeruleopunctatus	Aequidens coeruleopunctatus		Aequidens coeruleopunctatus	Aequidens coeruleopunctatus
			Archocentrus panamensis	Archocentrus panamensis
			Geophagus crassilabris	Geophagus crassilabris
	Vieja maculicauda	←	Vieja maculicauda	Vieja maculicauda
			Brachyrhaphis cascajalensis	Brachyrhaphis cascajalensis
Brachyrhaphis episcopi	Brachyrhaphis episcopi		Brachyrhaphis episcopi	Brachyrhaphis episcopi
Neoheterandria tridentiger	Neoheterandria tridentiger		Neoheterandria tridentiger	Neoheterandria tridentiger
Poecilia gillii	Poecilia gillii		Poecilia gillii	Poecilia gillii
Poeciliopsis elongata	Poeciliopsis elongata			
			Rivulus brunneus	Rivulus brunneus

Fig. 1: The Panama Canal Experiment. Species that colonized the Rio Grande from the Rio Chagres are depicted in the top left (moving up and to the right, they are *Brycon chagrensis*, *Brycon petrosus, Vieja maculicauda*, *Ancistrus chagresi* and *Roeboides guatemalensis*) and species that colonized the Rio Chagres from the Rio Grande are situated in the bottom right hand corner (moving down and to the left, they are *Astyanax aeneus*, *Roeboides occidentalis* and *Cyphocharax magdalenae*).

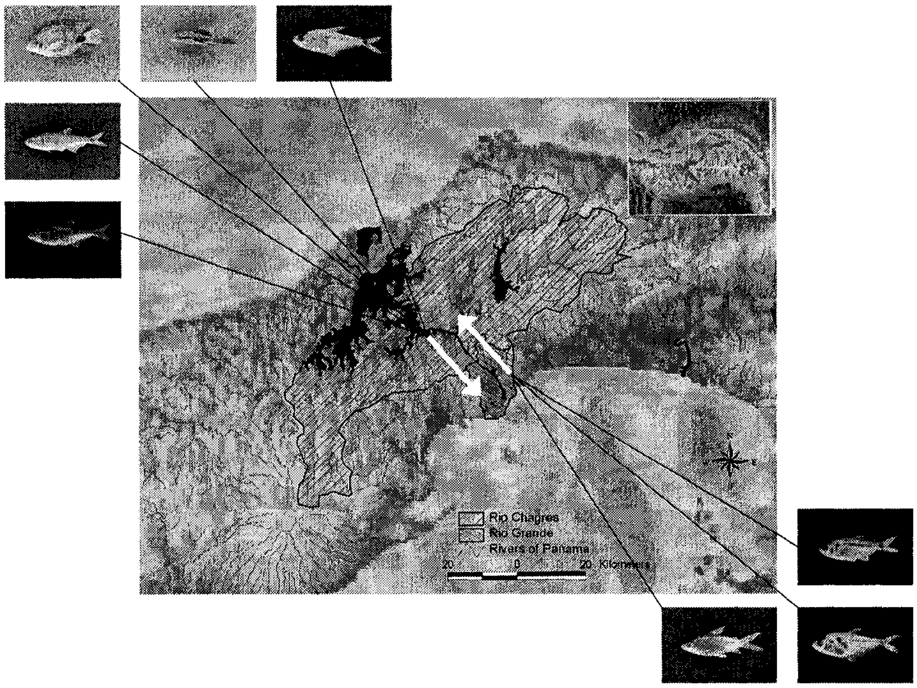
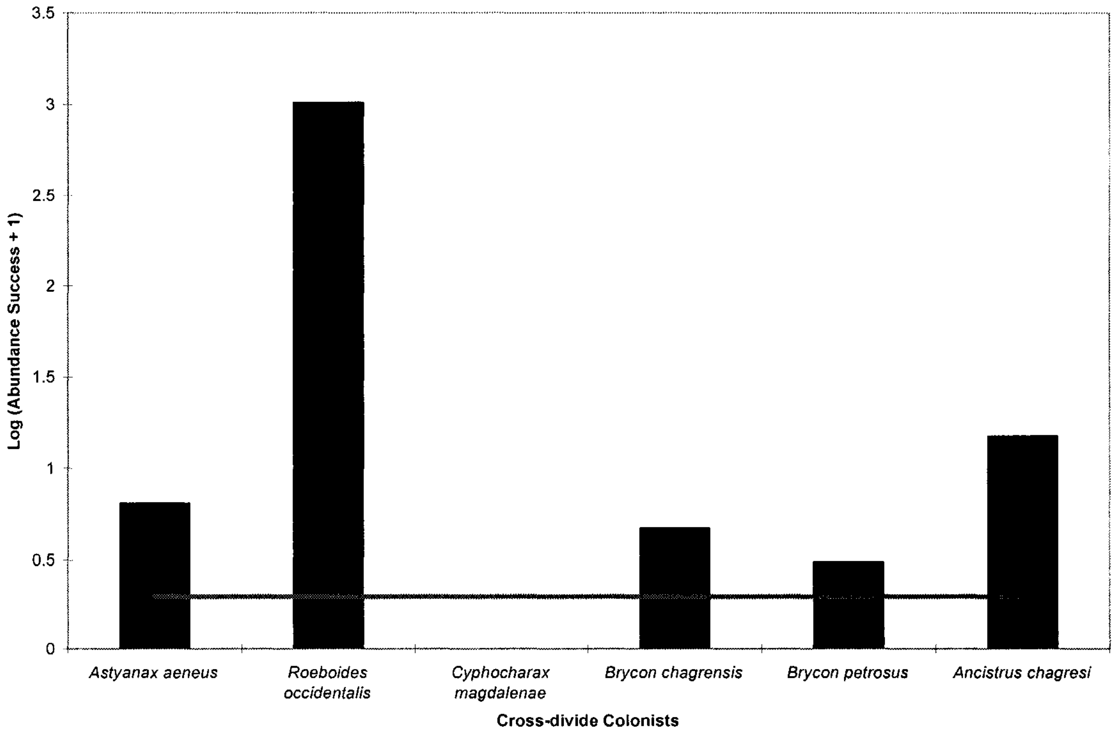
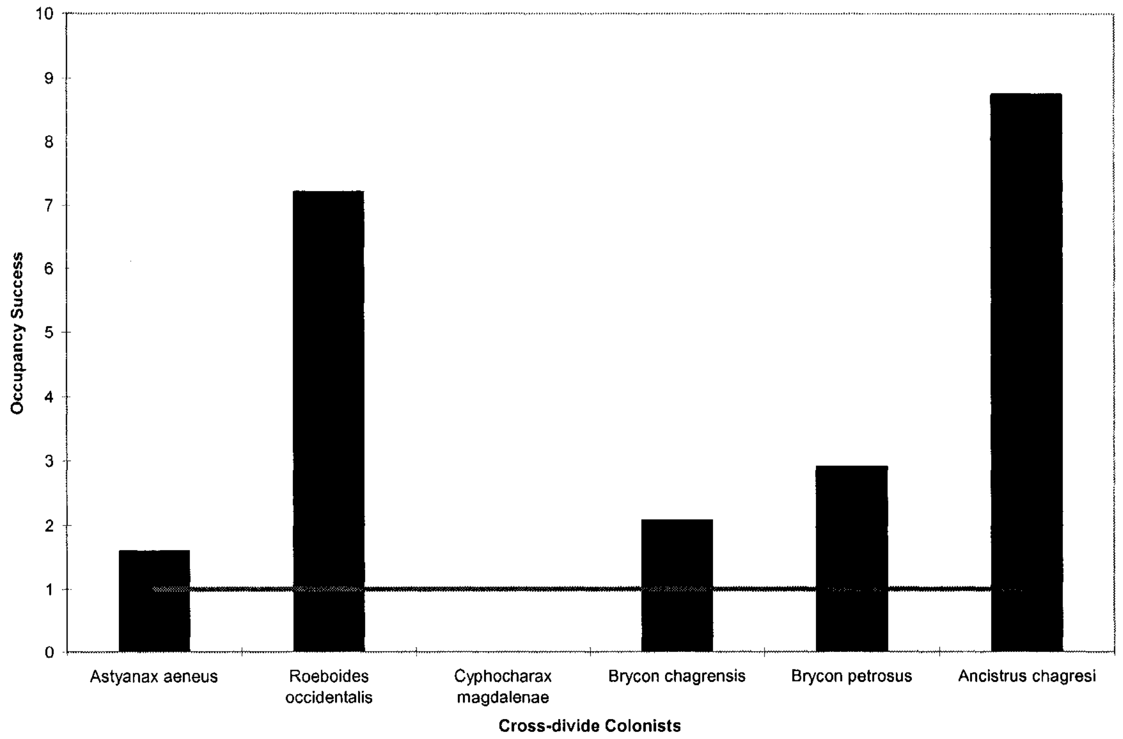


Fig. 2A, B: The abundance and occupancy success of primary and secondary freshwater fish colonists. Only cross-divide colonists for whom we have quantitative data were included in these figures. Abundance success was calculated by dividing the percentage of the total abundance of each colonist in its native drainage basin by that in its translocated drainage basin. The data were then log transformed to facilitate direct interpretation from the graph. Similarly, occupancy success was calculated by dividing the percent occupancy (or the number of sites occupied/number of sites in the sample) of colonists in their native drainage by that in their translocated drainage basin. The horizontal line bisecting the columns in both figures represents the value indicating equal abundance (or occupancy) success in the native and translocated drainage basins.




Occupancy Success
0
1
2
3
4
5
6
7
8
9
10
Astyanax aeneus
Roeboides occidentalis
Cyphocharax magdalenae
Brycon chagrensis
Brycon petrosus
Ancistrus chagresi
Cross-divide Colonists

Supporting Online Material

Table S1: The primary and secondary freshwater fish communities of the Rio Grande and Rio Chagres drainage basins, including those species that were not originally collected by Meek and Hildebrand (13). Colonists and the direction of colonization are indicated by the arrows depicted in the Direction of Migration column. * *Cyphocharax magdalenae* was not captured by Meek and Hildebrand (13), however, the authors captured it in the drainage basins adjacent to the Rio Grande and concluded that it was indeed part of the pre-1914 fauna of the Rio Grande. In addition, the geographic distribution of *Cyphocharax magdalenae* suggests that this species migrated through the Panama Canal. ***Brachyhypopomus occidentalis* was not captured in the Rio Grande by Meek and Hildebrand (13), probably owing to both its rarity and the difficulties involved in collecting this fish, and consequently we have not considered this species as a cross-divide colonist. ***Indicates species that were not recorded in Meek and Hildebrand's (13) survey, however, whose geographic distribution (14) suggests that these species might represent post-Canal additions to the Rio Chagres and the Rio Grande.

Pre-1914 Rio Grande	*Present-Rio Grande*	*Direction of Migration*	*Present-Rio Chagres*	*Pre-1914 Rio Chagres*
			Astroblepus trifasciatum	
Astyanax aeneus	Astyanax aeneus	→	Astyanax aeneus	
Astyanax ruberrimus	Astyanax ruberrimus		Astyanax ruberrimus	Astyanax ruberrimus
	Brycon chagrensis	←	Brycon chagrensis	Brycon chagrensis
	Brycon obscurus***		Brycon obscurus	
	Brycon petrosus	←	Brycon petrosus	Brycon petrosus
Bryconamericus emperador	Bryconamericus emperador		Bryconamericus emperador	Bryconamericus emperador
Compsura gorgonae	Compsura gorgonae		Compsura gorgonae	Compsura gorgonae
Gephyrocharax atricaudata	Gephyrocharax atricaudata		Gephyrocharax atricaudata	Gephyrocharax atricaudata
			Hyphessobrycon panamensis	Hyphessobrycon panamensis
			Pseudocheirodon affinis	Pseudocheirodon affinis
Roeboides occidentalis	Roeboides occidentalis	→	Roeboides occidentalis	
	Roeboides guatemalensis	←	Roeboides guatemalensis	Roeboides guatemalensis
Cyphocharax magdalenae*	Cyphocharax magdalenae	→	Cyphocharax magdalenae	
Hoplias microlepis	Hoplias microlepis		Hoplias microlepis	Hoplias microlepis
Piabucina panamensis	Piabucina panamensis		Piabucina panamensis	Piabucina panamensis
	Ancistrus chagrensis	←	Ancistrus chagrensis	Ancistrus chagrensis
			Chaetostoma fischeri	Chaetostoma fischeri
Hypostomus panamensis	Hypostomus panamensis		Hypostomus panamensis	Hypostomus panamensis
			Leptoancistrus canensis	
			Rineloricaria uracantha	Rineloricaria uracantha
			Imparales panamensis***	
Pimelodella chagresi	Pimelodella chagresi		Pimelodella chagresi	Pimelodella chagresi
Rhamdia quelen	Rhamdia quelen		Rhamdia quelen	Rhamdia quelen
	Brachyhypopomus occidentalis**		Brachyhypopomus occidentalis	Brachyhypopomus occidentalis
			Trichomycterus striatus	
			Rivulus brunneus	Rivulus brunneus
Aequidens coeruleopunctatus	Aequidens coeruleopunctatus		Aequidens coeruleopunctatus	Aequidens coeruleopunctatus
			Archocentrus panamensis	Archocentrus panamensis
			Geophagus crassilabris	Geophagus crassilabris
	Vieja maculicauda	←	Vieja maculicauda	Vieja maculicauda
			Vieja tuyrensis***	
			Brachyrhaphis cascajalensis	Brachyrhaphis cascajalensis
Brachyrhaphis episcopi	Brachyrhaphis episcopi		Brachyrhaphis episcopi	Brachyrhaphis episcopi
Neoheterandria tridentiger	Neoheterandria tridentiger		Neoheterandria tridentiger	Neoheterandria tridentiger
Poecilia gillii	Poecilia gillii		Poecilia gillii	Poecilia gillii
Poeciliopsis elongata	Poeciliopsis elongata			
	Priapichthys dariensis			
	Synbranchus marmoratus		Synbranchus marmoratus	

General Conclusions

The main objective of this thesis was to identify the relative importance of regional and historical processes, at varying spatial scales, to patterns of community composition and species richness of Mesoamerican freshwater fish communities. The study of the patterns of distribution and diversity of LMA fishes permits several general conclusions to be made regarding the nature of processes governing the assembly and maintenance of biological communities. Although I examined two sets of patterns at very different spatial scales, both studies highlight the importance of regional and historical processes to the patterns of the distribution and diversity of organisms observed at the local scale.

Diversity anomalies in matched communities in different regions provide one of the best lines of evidence that history imparts a powerful imprint on the composition and species richness of local communities. Comparison of diversity anomalies between communities of freshwater fishes in eastern Panama and northern Costa Rica suggests that differential patterns of community composition and species richness arise as a result of the unique historical circumstances that surrounded the colonization of LMA. The differential geographic success (both in terms of dispersal and diversification) of primary and secondary freshwater fishes provides strong evidence that the biology of organisms is an important determinant of the patterns of distribution and diversity of biological communities. The geologic evolution of the LMA Isthmus coupled with the differential salinity tolerance of freshwater fish families played a very important role in the colonization history of LMA. It is interesting to note, however, that salinity tolerance has no effect on the size of species' geographic ranges, suggesting that the dispersal of secondary fishes along coastlines occurs infrequently, even over evolutionary time scales. Nevertheless, history has left an important imprint on the freshwater fish fauna of LMA. Furthermore, our results, viewed in light of the hypotheses proposed in Martin and Bermingham (1998) and Bermingham and Martin (1998), indicate that the filtering effect of barriers changes in space (distance from source populations) and over time. The nascent Isthmus presented early freshwater fishes colonists with unique historical opportunities to disperse across an undeveloped landscape. Subsequent colonization events from South America, however, met increasing resistance as a consequence of the geologic evolution of the LMA landscape. Another plausible explanation for differential temporal colonization success is that increasing species richness acted to retard the expansion of later arriving species. The results presented in Chapter #2 that local communities of freshwater fishes in lower Mesoamerica were not resistant to invasion, nor were they vulnerable to extinction following invasion, however, suggest that geological processes rather than local deterministic processes were more important in determining the dispersal success of colonists participating in different colonization events. Finally, our results suggest that freshwater fishes are extremely dispersal limited.

On a smaller spatial scale, the natural experiment of the Panama Canal provides an unusually convincing test of ecological theory by describing the outcome of a natural experiment of unprecedented magnitude. Completion of the Panama Canal in 1914 breached the continental divide, and thus dramatically increased the likelihood of dispersal between previously isolated freshwater fish communities without affecting environmental variables. The results of this natural experiment clearly contradict the view that the fish communities of this region were saturated with species specifically adapted to local conditions. The communities were not resistant to invasion, nor were they vulnerable to extinction following invasion. Rather, my results are consistent with the predominance of regional effects, in which ecological differences between species are largely over-ridden by immigration, and are even consistent with strictly neutral community models in which no such differences exist. The value of this large-scale unintentional experiment is that it provides, for this situation, a clear answer to a question that has long been inconclusively debated.

Regional and historical processes have left an important imprint on the freshwater fish fauna of LMA at two distinct spatial scales. The importance of regional and historical processes is unparalleled at both the regional and continental scale. My results permit the inference that regional and historical processes have a primary influence on the distribution and diversity of Mesoamerican freshwater fish communities, and that the ecological interactions among species are not independent of a region's history. The interactions among species in any given community are defined by the historical events responsible for the assembly of that fauna. Thus, results presented herein permit the inference that regional and historical processes probably play an ongoing role in the maintenance of LMA freshwater communities.

The conclusions of this thesis have a direct bearing on the study of the world's biological diversity. My results suggest that ecologists need to study patterns and processes at much larger spatial scales in order to understand the driving mechanisms behind the patterns of biological diversity observed in nature. Moreover, the decisive results of the Panama Canal experiment highlight the strength of the experimental method in distinguishing between competing hypotheses and support its increased use in community ecology in order to try to better understand the processes that are responsible for the distribution and diversity of organisms. Experimental manipulations, however, will prove difficult owing to the difficulty in manipulating variables at such large spatial scales, as well as the ethical problems arising from such manipulations. Ecological realistic laboratory microcosms do not suffer from the same constraints, and thus present an interesting means by which community ecologists can investigate ecological theory.

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