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INSTITUTO DE ECOLOGÍA

BIOGEOGRAFÍA Y MACROECOLOGÍA DE PECES DULCEACUÍCOLAS Y SUS HELMINTOS EN MÉXICO

T E S I S

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

P R E S E N T A

LORENA GARRIDO OLVERA

TUTOR PRINCIPAL DE TESIS:

DR. HÉCTOR TAKESHI ARITA WATANABE (CENTRO DE INVESTIGACIONES EN ECOSISTEMAS)

COMITÉ TUTOR:

DR. GERARDO PÉREZ PONCE DE LEÓN (INSTITUTO DE BIOLOGÍA)

DR. LUIS ZAMBRANO GONZÁLEZ (INSTITUTO DE BIOLOGÍA)

MÉXICO, D.F. **FEBRERO, 2013.**

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Director General de Administración Escolar, UNAM
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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 26 de noviembre de 2012, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **GARRIDO OLVERA LORENA** con número de cuenta **97556099** con la tesis titulada: **"BIOGEOGRAFÍA Y MACROECOLOGÍA DE PECES DULCEACUÍCOLAS Y SUS HELMINTOS EN MÉXICO",** realizada bajo la dirección del DR. HÉCTOR TAKESHI ARITA WATANABE**:**

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 12 de febrero de 2013.

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
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c.c.p. Expediente de la interesada.

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RESUMEN

La mayoría de los estudios en biogeografía y macroecología involucran a vertebrados terrestres y plantas vasculares, mientras que muchos organismos más pequeños y otros sistemas han recibido poca atención. Para contribuir al conocimiento de los sistemas dulceacuícolas en estos campos de investigación, en el presente trabajo se describen patrones de distribución geográfica de los peces dulceacuícolas nativos de México y de sus helmintos adultos y se determinan las posibles causas que los generaron y/o modificaron. El trabajo se dividió en dos capítulos, cada uno conformado como un artículo de publicación con su formato respectivo.

En el primer artículo se documentaron los patrones de riqueza de especies, tamaño corporal y tamaño de las áreas de distribución de los peces dulceacuícolas mexicanos. Para cada especie se obtuvo el tamaño del cuerpo y su distribución geográfica a nivel de región hidrológica. Se construyeron histogramas para examinar las distribuciones de las frecuencias del tamaño de las áreas de distribución y el tamaño del cuerpo. Se evaluó la relación entre la latitud y esas dos variables con modelos de regresión lineal, en los que se controlaron los posibles efectos filogenéticos por usar los valores de los contrastes independientes de las variables macroecológicas. Se determinó que factores generan y/o modifican la variación espacial de la riqueza de especies a través de regresiones múltiples, donde la variable de respuesta fue la riqueza especies y las variables explicativas fueron características geográficas, ambientales e históricas de las regiones hidrológicas. La ictiofauna dulceacuícola mexicana incluye aproximadamente 420 especies pertenecientes a 26 familias, que se distribuyen en 34 de las 37 regiones hidrológicas. Las distribuciones de frecuencia tanto del tamaño corporal como del tamaño del área de distribución fueron sesgadas a la derecha, indicando que la mayoría de las especies de peces son pequeñas y que sus áreas de distribución son reducidas. Los análisis de variación espacial mostraron que ambas variables tienden a decrecer hacia latitudes bajas, revelando que las reglas de Rapoport y Bergmann se extienden a este ensamblaje de peces. La riqueza de especies también varió a lo largo de las regiones hidrológicas y se determinó que los factores más importantes en la conformación del patrón son los procesos históricos (eventos de vicarianza y tasas de especiación elevadas), mientras que las variables relacionadas con el área del hábitat contribuyen al mantenimiento de tales gradientes espaciales.

En el segundo artículo se describieron los patrones de distribución de la riqueza de helmintos de los peces dulceacuícolas mexicanos (a través de los grupos de parásitos y huéspedes

y de las regiones hidrológicas) y se evaluaron los efectos de las características del huésped y de su área de distribución en la riqueza de especies de helmintos. Para ésto se construyó una base de datos con los registros de los helmintos (trematodos, cestodos, monogeneos, acantocéfalos, nematodos e hirudineos). El análisis de esta información mostró que este grupo de parásitos se compone de 160 especies, que en estado adulto parasitan a 149 especies de peces que pertenecen a 23 familias distribuidas en 21 regiones hidrológicas. La riqueza de helmintos varió a través de los grupos de parásitos y huéspedes y de las regiones hidrológicas. Los nematodos fueron el grupo más rico, con aproximadamente 50 especies, mientras que otros grupos se componen de menos de 10 especies (Hirudinea, Acanthocephala y Cestoda). La familia de huéspedes que albergó el conjunto más rico de helmintos fue Cichlidae, mientras que Atherinopsidae y Goodeidae mostraron asociaciones de parásitos relativamente pobres. La riqueza de helmintos en las regiones del sureste de México fue más alta que en las regiones del norte o centro. Para examinar que factores generaron y/o modificaron la variación de la riqueza de especies de helmintos entre las especies de peces se usaron modelos de regresión múltiple, en los que se ingresaron los valores de las variables o los valores de los contrastes independientes de estas variables para controlar los posibles efectos filogenéticos. En ambos casos se determinó que el tamaño del área de distribución del huésped es el predictor más importante de la riqueza de helmintos (los peces con distribución más amplia poseen conjuntos de parásitos más ricos). Sin embargo, las interacciones entre esta variable y otras tales como el nivel trófico, la latitud, la temperatura y la precipitación del hábitat también son importantes.

En la discusión general del presente trabajo se señala que los resultados corroboran la generalidad de algunos patrones y teorías macroecológicas. La mayoría de las especies de peces dulceacuícolas mexicanos tienen tamaños corporales pequeños y sus áreas de distribución son reducidas. Las reglas de Rapoport y Bergmann también se cumplen para este ensamblaje de especies. Los factores que determinan la variación geográfica de la riqueza de especies de peces dulceacuícolas de México y la de sus helmintos apoyan las hipótesis especies-área y especies-energía. Sin embargo, se reconoce que la posición biogeográfica del país y el aislamiento geográfico de sus cuencas son los factores más importantes induciendo la variación espacial de la riqueza de especies de los peces al menos a nivel de regiones hidrológicas.

ABSTRACT

Most biogeographical and macroecological studies concern terrestrial vertebrates and vascular plants, while many small-sized taxa and other systems have received little attention. In order to expand the knowledge of freshwater systems in both research fields, in this survey we describe the geographical distribution patterns of native Mexican freshwater fish and of their adult helminths and we determine the possible causes that generated and/or modified them. The thesis is divided on two main chapters, each representing a paper with its respective format.

The first paper documented patterns in species richness, body size and geographical range size of Mexican freshwater fishes. For each species was obtained body size and geographical distribution at level of hydrological region. Histograms were built to examine the frequency distributions of geographical range size and body size. The relationships between latitude and these two variables were assessed with linear regression models, where potential phylogenetic effects were controlled by using independent contrast values of the macroecological variables. In order to determine the factors responsible for spatial variation pattern of species richness multiple regressions were used, where response variable was species richness and explanatory variables were geographic, environmental and historical characteristics of hydrologic regions. The Mexican freshwater ichthyofauna includes approximately 420 species of 26 families distributed in 34 of the 37 hydrologic regions. The frequency distributions of geographical range size and body size were right-skewed, indicating that most of the species are small-body and their geographical ranges are narrow. The spatial variation analysis showed the two variables have a tendency to decrease towards lower latitudes, revealing that Rapoport's and Bergmann's rules also extend to this fish assemblage. Species richness also varied along hydrological regions and it was found that the most important factors in shaping of the pattern are historical processes (vicariance events and high speciation rates), while area-related variables contribute to maintain such species richness gradients.

The second paper documented the distribution patterns of helminth richness of Mexican freshwater fishes (along groups of parasites and hosts and hydrologic regions) and evaluated the effects of host and its distribution range characteristics on helminth species richness. We built a database with records of helminths (trematodes, monogeneans, cestodes, acanthocephalans, nematodes, and hirudineans). The analysis of the information showed this parasite group includes 160 species parasitizing as adults 149 fish species of 23 families distributed in 21 regions. The

helminth richness varied across parasite and host groups and hydrologic regions. Nematoda was the richest group, with approximately 50 species, while other groups included less than 10 species (Hirudinea, Acanthocephala and Cestoda). Cichlidae harboured rich helminth assemblages, while Goodeidae and Atherinopsidae showed relatively poor parasite assemblages. Helminth richness in southeastern Mexico was higher than northern or central regions. Multiple regressions were used to determine the factors that generated and/or modified spatial variation of helminth species richness. The models included variables values or independent contrasts values of these variables to control for possible phylogenetic effects. In both cases it was found that distribution range size was the most important richness predictor (widespread fishes harbour richer parasite assemblages). However, the interactions between this variable and others such as trophic level, latitude, temperature and precipitation are important.

In the general discussion of this study it is pointed out that the results corroborate the generality of certain macroecological patterns and theories. Most of freshwater fish species of Mexico are small-bodied and rare in occurrence. Rapoport's and Bergmann's rules also extend to this fish assemblage. The factors determining the geographic variation of species richness of Mexican freshwater fishes and of their helminths (i. e., among host species) support species-area and species-energy hypothesis. However, it is recognized that biogeographical position of the country and geographic isolation of their drainage basins are the most important factors inducing the spatial variation of fish species richness.

INTRODUCCIÓN GENERAL

Los patrones de distribución geográfica de la biota y las causas que los han producido y/o modificado son objeto de estudio de la biogeografía y más recientemente de la macroecología (Brown, 1995; Llorente-Bousquets *et al*., 2001). La biogeografía identifica y descubre patrones que involucran la congruencia no azarosa de las distribuciones de taxones distintos: el endemismo y la disyunción (Espinosa-Organista *et al*., 2002; Escalante *et al*., 2003), mientras que la macroecología estudia los patrones de variación espacial de la biodiversidad usando como medida a la riqueza de especies o bien otras facetas de la biodiversidad principalmente relacionadas con la diferencia entre los taxones tales como las áreas de distribución, el tamaño corporal y la abundancia (Kent, 2005; Smith *et al*., 2008).

La mayoría de los estudios en estos campos de investigación han involucrado vertebrados terrestres y plantas vasculares, pero estudios tratando organismos más pequeños y/o taxones dulceacuícolas y/o marinos son escasos (Lomolino y Heaney, 2004; Storch y Gaston, 2004). En sistemas dulceacuícolas han dominado los estudios macroecológicos a grandes escalas y los peces han recibido una mayor atención (Heino, 2011). Los patrones más documentados para este tipo de peces son los de variación geográfica en el número de especies (Oberdorff *et al*., 2011), aunque patrones del tamaño corporal y del tamaño del área de distribución geográfica también son bien conocidos (Griffiths, 2010). Los gradientes latitudinales (disminución progresiva de la riqueza de especies a medida que se procede del ecuador hacia los polos) son los patrones de variación espacial mejor conocidos para peces dulceacuícolas y al menos tres hipótesis los han explicado: hipótesis especies-energía, hipótesis especies-área e hipótesis histórica (Oberdorff *et al*., 2011; Heino, 2011). La hipótesis especies-energía supone que a mayor energía disponible en el sistema, más biomasa y/o abundancia y por lo tanto mayor riqueza de especies. La hipótesis especies-área señala que a mayor área más habitas y refugios disponibles que facilitan la ocurrencia de poblaciones más grandes, índices de especiación altos e índices de extinción bajos. La hipótesis histórica propone que los sistemas de latitudes altas no han tenido tiempo suficiente para ser recolonizados después de los efectos de las glaciaciones en sus biotas, mientras que los hábitats de latitudes bajas no han sufrido cambios en sus biotas debido a la estabilidad de las condiciones climáticas durante el mismo periodo.

Otros organismos dulceacuícolas raramente han sido usados para dirigir cuestiones biogeográficas y macroecológicas (Heino, 2011). Sin embargo, los parásitos de peces

dulceacuícolas han recibido cierta atención en lo que a la variación espacial de la riqueza de especies (es decir, entre especies de huéspedes) se refiere. Poulin (2004) señala que la mayoría de estos estudios se han enfocan en predicciones de la teoría de biogeografía de islas, la teoría epidemiológica y/o los gradientes latitudinales (altas tasas de especiación en áreas en zonas tropicales, es decir, con temperaturas elevadas). Las dos primeras se sobrelapan grandemente, pero en general sugieren que el número de especies de parásitos es mayor en huéspedes con características que promueven la adquisición de nuevas especies a través de colonización o especiación (áreas de distribución amplias) o con atributos que proporcionen más espacios y otros recursos para los parásitos (tamaños corporales grandes). La última propone que la riqueza de especies parasitas es mayor en los trópicos que en las áreas templadas, debido a que las temperaturas elevadas se asocian con tiempos de generación más cortos e índices de mutación más altos y en consecuencia índices de especiación y evolutivos más altos. Las investigaciones con endoparásitos apoyan la teoría de biogeografía de islas o la teoría epidemiológica, reportando el tamaño del huésped y el de su área de distribución como los predictores de la riqueza de especies, mientras que el tamaño corporal del huésped y la latitud/temperatura parecen ser los determinantes principales de la riqueza de especies de ectoparásitos (Luque y Poulin, 2008).

Los estudios biogeográficos son escasos en ambientes dulceacuícolas, pero las tendencias actuales destacan la importancia de complementar los resultados de este tipo de estudios con los macroecológicos y viceversa, para identificar la operación y magnitud de los procesos tanto ecológicos como históricos que subyacen a la distribución de la biota (Wiens y Donoghue, 2004). Bajo este escenario y para contribuir al conocimiento biogeográfico y macroecológico en sistemas dulceacuícolas, en el presente trabajo se describen los patrones de distribución geográfica de los peces dulceacuícolas nativos de México y de sus helmintos adultos y se determinan las posibles causas que los generaron y/o modificaron usando análisis estadísticos comunes en macroecología pero incorporando factores no solo ecológicos si no también históricos.

CAPÍTULO I

ORIGINAL ARTICLE

MACROECOLOGICAL PATTERNS OF MEXICAN FRESHWATER FISHES

Lorena Garrido-Olvera[1], Luis Zambrano-González[2], Norman Mercado-Silva[3] and Gerardo Pérez-Ponce de León[2*]

[1]Posgrado en Ciencias Biológicas, Instituto de Ecología, Universidad Nacional Autónoma de México. Ciudad Universitaria, Apartado Postal 70-275, C. P. 04510, Distrito Federal, México. E-mail: lgarrido@ecologia.unam.mx

[2]Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. Ciudad Universitaria, Apartado Postal 70-153, C. P. 04510, Distrito Federal, México.

[3]Departamento de Ecología y Recursos Naturales, Centro Universitario de la Costa Sur, Universidad de Guadalajara. Independencia Nacional 151, Autlán de Navarro, C. P. 48900, Jalisco, México.

* Correspondence: Gerardo Pérez-Ponce de León, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. Ciudad Universitaria, Apartado Postal 70-153, C. P. 04510, Distrito Federal, México. E-mail: ppdleon@ibunam2.ibiologia.unam.mx

MACROECOLOGY OF FRESHWATER FISHES

For Peer Review

ABSTRACT

Aim To test whether patterns in species richness, geographical range size and body size of native Mexican freshwater fishes resemble those found for other freshwater fish assemblages and to determine the features responsible for the spatial variation in species richness.

Location Mexico

Methods For each fish species was compiled body size information and spatial distribution data at level of hydrological region. Histograms were built to examine the frequency distributions of geographical range size and body size. The relationships between latitude and geographical range size and body size were inspected with linear regression models, where independent contrast values of these macroecological variables were used to control for potential phylogenetic effects. Multiple regressions were used to investigate the geographic, environmental and historical factors affecting species richness.

Results The Mexican freshwater ichthyofauna comprised of approximately 420 species in 26 families distributed in 34 of the 37 hydrological regions. The frequency distributions of geographical range size and body size were right-skewed or approximately normal under logarithmic transformation. The geographical range size and body size of species have a tendency to decline towards lower latitudes. The most important factors shaping geographical distribution pattern of species richness are historical processes, while it seems that area-related variables only are contributing to the maintenance of this spatial gradient.

Main conclusions Most freshwater fish species of Mexico are small-bodied and rare in occurrence. Rapoport's and Bergmann's rules also extend to this fish assemblage. The biogeographical position of the country and geographic isolation of their drainage basins have induced the spatial variation of species richness.

Keywords

Geographical range size, body size, species richness, Rapoport's rule, Bergmann's rule, speciation rate, species-area relationship, latitudinal gradient, freshwater fishes, Mexico.

For Peer Review

INTRODUCTION

Macroecology highlights the statistical properties that emerge from complex ecosystems to identify general patterns particularly at large scales (Oberdorff *et al.*, 2011). The main statistical regularities that occur on these scales comprise patterns in the frequency distributions of particular variables (e.g. body size, abundance and geographical range size), the relationships between such variables and general patterns in species richness (Storch & Gaston, 2004). However, most studies concern terrestrial systems, whereas marine and freshwater systems have received considerably less attention (Heino, 2011).

The macroecological researches in the freshwater realm have mainly addressed questions in terms of species diversity patterns (e.g. latitudinal gradients in species richness and species turnover along geographical gradients) (Heino, 2011). One of the better known freshwater assemblages in this research field is represented by the North American freshwater fish fauna (Griffiths, 2010; Oberdorff *et al.*, 2011). For this fish group, three major hypotheses have been tested to explain the variability of species richness at large scales: the species-area hypothesis, the species-energy and the historical hypothesis. The first refers to the existence of a positive relationship between the number of species present in a given area and the size of this area. The second predicts a positive correlation between species richness and the energy available within the system, determining either resources availability or the physiological limits of the species. Finally, the historical hypothesis explains differences in richness gradients as a consequence of species potential for system recolonization, and thus by the maturity degree of systems achieved since the last major climate change or by the degree of stability in past climatic conditions (Oberdorff *et al.*, 2011).

Patterns in the frequency distributions of body size and geographical range size and in the relationships between latitude and these variables also have been documented for North American freshwater fishes. The geographical range size (latitudinal range) of species of this assemblage has showed a clear Rapoport effect, i.e. an increase in geographical range size with increasing latitude (Griffiths, 2010). Additionally, an increase in the mean body size of species with increasing latitude has been found (Bergmann's rule) (Knouft, 2004; Griffiths, 2011). In addition, the latitudinal changes in mean body size are accompanied by changes in the shape of frequency distributions of body size: body size distributions change from right- to left-skewed with increasing latitude (Griffiths, 2011).

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Datasets used to recognize macroecological patterns of North American freshwater fishes have included a high percentage of Nearctic species distributed in Mexico (e.g. Oberdorff *et al.*, 1997; Griffiths, 2010, 2011). However, no study has been conducted to only describe macroecological patterns of the Mexican freshwater fish fauna, even though the country has an extraordinary species richness, high level of endemisms and it is situated in a transitional biogeographical zone, where Nearctic and Neotropical biotic components overlap (Miller *et al.*, 2005). When relationships between latitude and geographical range size and body size of North American freshwater fishes were examined, the analyses assumed phylogenetic independence between data points (see Griffiths, 2010). Thus, the aforementioned patterns should be regarded as tentative with respect to data from Mexico. In order to expand our knowledge of macroecological patterns of Mexican freshwater fishes, the objectives of the present study are: 1) to document the patterns in species richness, geographical range size and body size of native Mexican freshwater fishes and 2) to determine the features responsible for the spatial variation in species richness.

MATERIALS AND METHODS

We assembled a database with distribution records for all Mexican freshwater fish species. Our study was restricted to the native fish species. Neither introduced species such as carps and tilapias nor species able to disperse across brackish and marine (e.g. eleotrids, centropomids) were included. The dataset was created from information in national and foreign ichthyological collections: Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México; Colección Ictiológica, Universidad Autónoma de Baja California; Colección Ictiológica, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León; Fish Collection, Tulane University Museum of Natural History; Fish Collection, University of Michigan Museum of Zoology; Fish Collection, Department of Zoology, University of Wisconsin. We also used personal collection information from N. Mercado-Silva and J. Lyons (University of Wisconsin – Madison, Department of Zoology). To avoid cases of synonymies, valid species names were used according to FishBase (Froese & Pauly, 2011).

In order to examine the frequency distributions of body size and geographical range size, the relationships between these variables and latitude, i.e. to test Rapoport's and Bergmann's rules, and general patterns of species richness, we gathered detailed information for each fish species and for each Mexican hydrological region where they

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are currently distributed. Miller *et al.* (2005) and Froese & Pauly (2011) were the primary sources of information for fish body size (maximum standard length expressed in cm). The environmental and geographic data for each hydrological region were obtained from the Comisión Nacional del Agua (2008) and Fernandez-Eguiarte *et al.* (2010).

For each fish species we calculated geographical range size and mean latitude of this range. The following characteristics were used as geographical range size measures: 1) latitudinal range (difference between maximum latitude and minimum latitude of occupied regions), 2) total basin length (sum of basin lengths of occupied regions in km), 3) area (sum of surfaces of the occupied regions in km^2), 4) total runoff (sum of mean natural superficial runoff of the occupied regions in millions of m^3/year) and 5) basin number (sum of the basins of the occupied regions). The mean latitude of a geographical range was determined as average between maximum latitude and minimum latitude of regional area.

Histograms were used to show frequency distributions of body size and geographical range size of species. Because the macroecological variables for closely related species are more similar than those of distantly related species, it is necessary to control for phylogenetic effects to test relationship between two traits (Gotelli & Taylor, 1999). In order to accomplish this, we computed independent contrasts (Felsenstein, 1985) for macroecological variables in the PDAP:PDTREE software (Midford *et al.*, 2011), implemented in Mesquite Modular System for Evolutionary Analysis, Mesquite version 1.12 (Maddison & Maddison, 2011). We constructed a composite phylogeny of the Mexican freshwater fish species, which was used to obtain independent contrasts (see Appendix S1 in Supporting Information). A composite phylogeny does not necessarily show the evolutionary process of speciation, but rather merely links species and clades. Thus, true branch lengths were not available in our tree, and all branch lengths were set to unity, which adequately standardized contrasts of all variables. Before contrasts were computed, we used a log-10 transformation on all variables, i.e. body size, geographical range size and mean latitude.

To test latitudinal trends in body size and geographical range size, the contrast values of these variables were regressed against contrast values of mean latitude. Because we were uncertain of the sign of the contrasts, we forced all the regressions through the origin (Garland *et al.*, 1992).

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Because species richness (the total number of species encountered within a hydrological region) may be confounded by uneven sampling area size, we corrected species richness values by taking the residuals of linear regression of species richness against the hydrological region area. Afterwards a map with the geographical distribution pattern of species richness was prepared using ArcView GIS 3.2 (ESRI, 1999) and multiple regression models were used to investigate the geographic, environmental and historical factors affecting species richness (Table 1). Following Oberdorff *et al.* (2011), we used endemic species number per hydrological region in order to analyze the role of historical processes in species richness distribution patterns, since their presence should reflect the roles of speciation, extinction, and dispersal ultimately responsible for their restricted geographic distribution. We used a log-10 transformation on all variables, and then, the minimal adequate model, i.e. models without redundant parameters, was obtained by fitting a maximal model and then simplifying it by stepwise deletion in which non-significant terms were left out, and significant terms were added back (Crawley, 2007). Statistical analyses were performed using the software R version 2.11.0 for Windows (http://www.r-project.org/).

RESULTS

The list of native Mexican freshwater fishes comprises approximately 420 species belonging to 26 families. This vertebrate group is distributed in 34 of the 37 hydrological regions. Hydrological regions of Baja California Centro-Este, Baja California Noreste and Mapimí did not have records (Fig. 1). The endemism level was high, because more than 60% of the species have been recorded only in Mexico (see Figs. S1-S7 in Appendix S1).

Poeciliidae was the most species-rich family with more than 82 species, while Batrachoididae, Bythitidae, Salmonidae, Sciaenidae, and Syngnathidae families were represented by only one species in Mexico (Figs. S1 & S5 in Appendix S1). No species occurred in all hydrological regions, but *Astyanax fasciatus* (Cuvier, 1819) and *Poecilia sphenops* Valenciennes, 1846 were distributed in 18 and 16 regions, respectively. In contrast, more than 200 species (approximately 50% of total species) were recorded only in one region.

The frequency distributions of body size and geographical range size were strongly right-skewed (or 'positively skewed'), but these were approximately normal

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under logarithmic transformation although with some skew. This means that most species are small-bodied and rare in terms of occurrence (Figs. 2 & 3).

The geographical range size and body size of species have a tendency to be larger toward higher latitudes than those of species toward lower latitudes, i.e. Mexican freshwater fishes follow the Rapoport´s and Bergmann´s rules, respectively (Table 2 & Fig. 4).

The residual species richness is not evenly distributed throughout the country. The hydrological regions with higher species richness were Coatzacoalcos, Grijalva-Usumacinta, Papaloapan and Pánuco, while in El Salado and the regions of the Baja California Peninsula and Sonora a lower number of species was recorded (Fig. 1). The minimal adequate model of the multiple regression explained more than 70% of variability of species richness. Only variables related with historical processes and region size were retained, with endemic species being the most important explanatory variable (Table 3, Fig. 5). We found a positive correlation between fish species richness and endemic species number and a positive correlation between the number of species present in a given region and the size of this region.

DISCUSSION

The study of the Mexican freshwater fish fauna has generally focused on species descriptions, the exploration of phylogenetic relationships in some groups, and descriptions some of their biological attributes, among other aspects. However, biogeographical and macroecological studies have never been assessed for overall species assemblage, preventing the large scale understanding of general patterns that arise from the combination of high species diversity in a territory with a very complex geological history. The present analysis has resulted in the identification of patterns in species richness, geographical range size and body size for native Mexican freshwater fishes.

Mexico has a rich and diversified freshwater fish fauna that includes approximately 500 native species (Miller *et al.*, 2005). However, we must note that that even though the species count provided in our study coincides with that provided by Pérez-Ponce de León & Choudhury (2010), it is not in agreement with previously published freshwater fish checklists where species counts are provided (e.g. Espinosa *et al.*, 1993; Miller *et al.*, 2005). This discrepancy arises in part from the challenge of defining what constitutes a freshwater fish (Miller *et al.*, 2005). Despite this difference,

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we consider that the results presented here are representative of the Mexican freshwater ichthyofauna, since more than 90% of species recorded in previous checklists are included in our analysis.

The frequency distributions of body size and geographical range size of Mexican freshwater fish species were similar to patterns held for most species assemblages (Storch & Gaston, 2004). Most fish species were small-bodied, and only a few were large-bodied. This pattern had been already uncovered for freshwater fish in other parts of the world (e.g. Fu *et al.*, 2004; Griffiths, 2006; Griffiths, 2011 and references therein). However, the shape of frequency distributions varies with spatial scale, biome, habitat structure, latitude, evolutionary history and trophic and taxonomic levels (Knouft, 2004). In addition, while early analyses assumed unimodal distributions, it has been evidenced that many body size distributions have more than one mode (Griffiths, 2011). A variety of hypotheses have been proposed to explain the shape of species body size distributions which can be classified as energetic, evolutionary, biogeographic, habitat structural and biotic (Allen *et al.*, 2006; Griffiths, 2011).

According to Storch & Gaston (2004) the frequency distributions of geographical range sizes differ with spatial scale. When the entire geographical range sizes of species are considered (a 'comprehensive' analysis), the distribution is approximately normal under logarithmic transformation although it commonly has with some left-skew. Comparatively, when an analysis is made within areas too small to embrace the entire geographic ranges of most of the species (a 'partial' analysis) the distribution is often more or less bimodal with many species occupying much of the geographical area. Our study reveals that most species of Mexican freshwater fishes were rare in their extent of occurrence or area of occupancy. This pattern was similar to results of a 'comprehensive' analysis (Storch & Gaston, 2004). However, many species that occur in Mexico could extend southwards or northwards beyond the area covered by the present study. Then, the pattern was highly influenced by the species that have been recorded only in Mexico (more than 60% of the total number of species in our analysis).

Methods that incorporate phylogenetic information into statistical analyses of the correlated evolution of continuous traits have become a common practice in the macroecological analysis of species assemblages (e. g. Luque & Poulin, 2008; Mandic *et al.*, 2009). However, these studies can be limited by a lack of robust phylogenies for many taxa. According to Garlan *et al.*, (1992), the Felsenstein's (1985) independent

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contrasts approach has been used in the absence of complete topological information. Some studies have used taxonomic information alone or in part to construct a phylogenetic topology, assuming that named taxa represent monophyletic groups. The use of such topologies can be misleading if the taxonomy does not follow a cladistic approach. However, they are useful to analyze the current data in the absence of phylogenetic information. In addition to that, we are totally aware that the Mexican freshwater fish phylogeny is not well-resolved since many polytomies are found leading to loss of information and of statistical power in the analyses. Despite the limitations of using a composite cladogram, our topology provided us with a hypothesis of species relationships that we were able to take into account before performing macroecological analyses on species-level attributes.

Contrast values of body size and geographical range size correlated positively with contrast values of mean latitude. This means that the dataset of Mexican freshwater fishes supports Bergmann´s and Rapoport´s rules. The increase in the body size of species with increasing latitude (Bergmann's rule) had already been described for freshwater fishes (e.g. Knouft, 2004; Griffiths, 2011), although only limited support had been found for Bergmann's proposed processes. In contrast, there has been much debate as to the generality of Rapoport's rule (the trend for the geographical range sizes of species to decline towards lower latitudes. The strongest evidence for Rapoport's rule come from the northern hemisphere, particularly between mid- to high latitudes, but it is not clear whether geographical range sizes are generally smaller in the tropics (Gaston *et al.*, 1998; Storch & Gaston, 2004).

With respect to species richness patterns, the results of our analysis reveal a significant influence of the historical processes (the biogeographical position of Mexico and geographic isolation of drainage basins), but also confirm previous findings concerning the effects of area-related variables at this spatial extent (species-area hypothesis). The overlap of Nearctic and Neotropical biotic components is particularly evident in southern and central Mexico (see Huidobro *et al.*, 2006), where hydrological regions possess higher fish species richness (e.g. Coatzacoalcos, Papaloapan, Grijalva-Usumacinta, Pánuco). Evidently, the sum of the elements of these biotic components results in an increase in fish species richness. Additionally, we must considerer that hydrological regions in southern and central Mexico are also richer essentially as a result of vicariance events associated with intense tectonic and volcanic activities (e.g. the Neovolcanic Axis or Transmexican Volcanic Belt, one of the most notable

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orographic features of this zone, characterized by extensive and complex geological processes). These changes are reflected in the fragmentation of the hydrological basins, which have influenced the evolution of freshwater fishes (Miller & Smith, 1986); empirical data on particular fish groups, such as goodeids, atherinopsids and cyprinids demonstrate the effect of the complex geological history, and the subsequent vicariant and dispersal events, on the diversification process of these fishes (see Domínguez-Domínguez *et al.*, 2006; Bloom *et al.*, 2009; Pérez-Rodríguez *et al.*, 2009).

The area hypothesis suggests that species richness has a tendency to increase with the size of the censused area and that the relationship is approximately linear on a log–log scale (Storch & Gaston, 2004). According to Oberdorff *et al.* (2011) several nonexclusive explanations have been proposed to explain the species-area relationship, but three of them are most often invoked: (1) the size dependent extinction rate, (2) the size dependent speciation rate, and (3) the diversity of the habitat. For the first explanation the probability of extinction of a species increases with a reduction in the size of the "island", due to a decrease in its population size. The second explanation suggests a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers. The third explanation suggests that the habitat heterogeneity and the diversity of available food resources increase with the size of the "island". These characteristics offer a large number of available niches and consequently favor the coexistence of a large number of species. Our data clearly support the second and third hypotheses because the richer regions, i.e. Coatzacoalcos, Papaloapan, Grijalva-Usumacinta and Pánuco, have a more dynamic history that favors positively speciation rates (see Huidobro *et al.*, 2006). Likewise, these regions possess the highest runoffs offering a large number of available niches.

When the historical variable (endemic species) was excluded from the multiple regression, the area-related variables and latitude were retained in the minimal adequate model, being latitude the most important explanatory variable. The negative relationship between fish species richness and latitude indicates that the diversity decreases from the tropics to the poles as in the vast majority of taxa, including freshwater fish from temperate regions (e.g. Oberdorff *et al.*, 1997). There is still much debate on whether the causes driving this pattern are biotic or abiotic and on the interdependence of many of the proposed explanatory hypotheses (Hillebrand, 2004). Evolutionary and historical hypotheses have received the strongest support; particularly those relating higher speciation rates (and/or lower extinction rates) in the tropics with higher historical

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stability that in turn allow higher clade persistence at lower latitudes (Rohde, 1992). However, the species-energy hypothesis, i.e. positive correlation between species richness and the energy available within the system, also has received significant support. Energy availability can influence fish species richness via two rather different processes: 1) energy can determine resources available for a given biological community and thus is productivity factor per se (Oberdorff *et al.* 1995; Guégan *et al.* 1998), and 2) energy can determine the physiological limits of the species (Oberdorff *et al.* 1995). In the former, a variable such as net primary production must be an important predictor of species richness. Whereas in the later, variables linked with temperature or available solar energy would predominate. For Mexican freshwater fishes, the temperature should help to explain the latitudinal gradient in species richness, because the hydrological regions that harbor more species, i.e. Coatzacoalcos, Papaloapan, Grijalva-Usumacinta and Pánuco, are closer to the equator and show the highest temperatures.

In spite of the limitations we refer above, we believe that the patterns we describe are sufficiently strong and that the main conclusions are unlikely to change in the future. While several aspects of the Mexican ichthyofauna are well understood at a local or regional level, our results provide large-scale perspectives that should open new avenues of research to understand other patterns in the freshwater fish fauna of tropical areas. However, we propose that future studies should incorporate a complete phylogeny with branch length estimates, which could magnify or diminish phylogenetic correlations between species traits.

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SUPPORTING INFORMATION

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

Appendix S1 Composite phylogeny of the Mexican native freshwater fishes.

BIOSKETCH

Lorena Garrido-Olvera is a PhD student in the Universidad Nacional Autónoma de México. Her research interests include distribution and diversity of freshwater fishes and their parasites in America.

Luis Zambrano González conducts research on aquatic ecology, restoration of freshwater systems, ecosystem services and aquatic and urban sustainability.

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Norman Mercado-Silva is professor at the Universidad de Guadalajara and a research specialist at the University of Arizona. His research focuses on fish ecology, invasive species in freshwater ecosystems and biomonitoring.

Gerardo Pérez-Ponce de León is researcher in the Instituto de Biología, Universidad Nacional Autónoma de México. His major research interests are the biodiversity, phylogenetics and historical biogeography of helminth parasites of freshwater fishes. Current projects include the use of molecular markers for finding cryptic species of helminths to contribute to the inventory of this group of parasitic organisms.

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Table 1 Geographic, environmental, and historical characteristics of Mexican hydrological regions.

Region	Fishes	Endemics	ML	LtR	LnR	Area (km^2)	Length (km)	Runoff (millions of m^3/year)	Basins	Neighbors	Slope	MAP (mm)	PDM (mm)	PWM (mm)	MTWM (°C)	MTCM (°C)
1	8		31.11	3	2.42	28492	9964	359	109	3	1	249.4	0.07	16.36	40.01	4.75
2	3		28.07	3.68	3.37	44314	12755	449	148	4	1	100.9	0.48	26.88	35.17	4.01
3	8		24.77	3.78	2.55	29722	9069	318	72	3	1	184.7	0.53	49.19	30.56	3.25
4	-	-	31.26	2.73	1.41	14418	4434	105	51	4	1	180.7	2.21	59.41	36.79	3.68
5	-	-	28.30	3.33	2.71	13626	4195	54	171	4	1	100.5	4.59	81.48	34.04	2.07
6	3		24.89	4.03	2.6	11558	6244	219	243	2	1	284.7	8.36	93.65	34.13	3.22
7	23		32.15	1.15	1.8	6911	2469	1863	3	3	1	100.3	4.62	137.86	35.71	3.96
8	11		30.66	3.61	4.97	61429	12376	139	54	2	1	301.2	0.07	25.17	35.03	6.58
9	40	8	28.97	4.73	5.19	139370	39635	4935	48	4	1	507.2	0.11	22.80	34.55	7.21
10	37	13	25.72	4.83	4.12	103483	37030	14408	49	4	1	715.9	4.39	69.05	33.30	2.30
11	47	19	23.44	3.49	3.09	51717	19704	7956	9	3	1	815.2	7.36	215.91	32.88	5.88
12	93	63	21.24	4.36	6.16	132916	51096	13637	8	8	1	723.2	0.37	81.02	34.33	9.51
13	24	13	21.05	1.51	0.98	5225	2658	1277	64	3	1	1396.2	0.21	45.88	33.84	9.70
14	45	15	20.68	1.21	1.82	12255	6132	2236	1	4	1	122.7	4.34	92.20	32.49	3.21
15	26	13	19.67	1.57	1.75	12967	6307	3684	45	3	1	1185.5	16.30	153.35	34.47	8.83
16	42	15	19.52	1.86	1.69	17628	7393	3882	8	5	1	911.3	7.28	71.58	30.69	4.16
17	14	5	18.45	1.05	1.51	9205	4218	1635	57	2	1	890.9	4.25	217.04	29.40	6.47
18	63	39	18.51	2.97	6.12	118268	45372	1757	3	8	1	949.7	15.22	184.34	30.82	7.72
19	21	6	17.42	1.44	2.49	12132	4992	691	41	2	1	1232.0	5.27	182.06	29.94	4.83
20	31	11	16.80	1.64	3.81	39936	12907	18714	21	5	1	1393.1	42.26	288.22	30.45	11.11
21	22	4	15.99	0.64	2.59	10514	3505	3389	48	2	1	971.2	3.33	367.16	31.89	12.32
22	26	5	16.61	0.83	2.46	16363	6042	2606	10	6	1	824.9	25.46	182.73	34.36	16.66
23	21	4	15.54	2.01	2.4	12293	3908	12554	25	2	1	2352.7	5.46	261.16	31.43	8.25
24	108	33	28.31	6.92	10.59	229740	77898	5156	2	7	2	448.5	2.82	318.30	33.27	13.73

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25	49	12	24.02	3.48	2.93	54961	16729	4328	27	3	2	758.5	4.27	224.06	31.37	10.11
26	89	52	21.50	4.91	3.59	96989	34263	20329	2	5	2	889.2	34.07	200.23	33.66	16.87
27	51	16	20.84	2.72	2.13	26592	10139	14306	38	3	2	1423.2	4.08	216.68	32.42	10.13
28	84	31	18.34	2.81	3.15	57355	19382	49951	31	5	2	1447.1	22.85	220.73	35.28	15.79
29	80	18	17.54	1.81	2.54	30217	8866	39482	10	3	2	1953.8	28.39	344.94	30.99	12.36
30	101	23	17.10	3.6	4.48	102465	23249	117546	4	4	2	1708.9	38.47	326.82	32.86	15.17
31	33	5	18.89	2.16	2.01	25443	1704	591	6	3	2	1227.4	2.78	272.12	31.39	12.94
32	47	17	20.62	1.98	3.77	58135	523	1	1	2	2	192.4	45.93	424.76	33.66	16.71
33	41	8	18.96	2.29	2.25	38308	2926	1989	2	2	2	1239.8	2.80	323.08	33.58	17.24
34	23	4	29.88	3.8	4.24	90829	19574	1701	20	2	3	407.8	4.43	310.47	32.35	11.94
35	-	-	27.37	3.6		62639	15503	957	17	2	3	355.7	6.48	220.89	30.93	13.39
36	35	15	24.64	3.93	4.87	9332	31046	1912	1	7	3	422.1	7.30	457.02	34.10	16.70
37	7	7	23.61	3.6	3.48	87801	17152	2637	22	5	3	428.2	2.88	253.71	32.31	14.40

The codes for the hydrological regions are as follows: 1=Baja California Noroeste, 2=Baja California Centro Oeste, 3= Baja California Suroeste, 4=Baja California Noreste, 5=Baja California Centro Este, 6=Baja California Sureste 7=Río Colorado, 8=Sonora Norte, 9=Sonora Sur, 10=Sinaloa, 11=Presidio-San Pedro, 12=Lerma-Santiago, 13=Río Huicicila, 14=Río Ameca, 15=Costa de Jalisco, 16=Armería-Coahuayana, 17=Costa de Michoacán, 18=Balsas, 19=Costa Grande de Guerrero, 20=Costa Chica de Guerrero, 21=Costa de Oaxaca, 22=Tehuantepec, 23=Costa de Chiapas, 24=Bravo-Conchos, 25=San Fernando-Soto La Marina, 26=Pánuco, 27=Norte de Veracruz, 28=Papaloapan, 29=Coatzacoalcos, 30=Grijalva-Usumacinta, 31=Yucatán Oeste, 32=Yucatán Norte, 33=Yucatán Este, 34=Cuencas Cerradas del Norte, 35=Mapimí, 36=Nazas-Aguanaval; 37=El Salado. Fishes= Fish species richness; Endemics=Endemic species number; ML=Mean latitude; LtR=Latitudinal range; LnR=Longitudinal range; Area=Area; Length=Total length of rivers; Runoff= Mean natural superficial runoff; Basins=Basin number; Neighbors=Neighbor region number; Slope: 1=Pacific, 2=Atlantic, 3=Interior; MAP=Mean annual precipitation; PDM=Precipitation of driest month; PWM=Precipitation of wettest month; MTWM=Maximum temperature of warmest month; MTCM=Minimum temperature of coldest month.

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Table 2 Latitudinal trends in body size and geographical range size of Mexican freshwater fishes. In all cases the explanatory variable was mean latitude.

Response variable	Slope	Error	t value	P value	R
Body size	0.42	0.2	2.12	0.03	0.01
Latitudinal range	1.99	0.21	9.31	<2 e-16	0.18
Total basin length	2.32	0.49	4.73	3.04 e-6	0.05
Area	2.22	0.34	5.56	5.03 e-8	0.07
Total runoff	-3.75	0.92	-4.08	5.47 e-5	0.04
Basin number	1.37	0.65	2.10	0.04	0.01

Table 3 Minimal adequate model of the multiple regression relating species richness to geographic, environmental and historical variables. Logarithmic transformations of variables were used in all cases. Adjusted R-squared 0.738.

Variable	Estimate	Standard Error	t value	P
(Intercept)	0.714	0.358	1.996	0.0554
Basin number	-0.213	0.079	-2.692	0.0117
Total basin length	-0.419	0.107	-3.913	0.0005
Total runoff	0.239	0.057	4.160	0.0003
Endemics	0.443	0.117	3.795	0.0007

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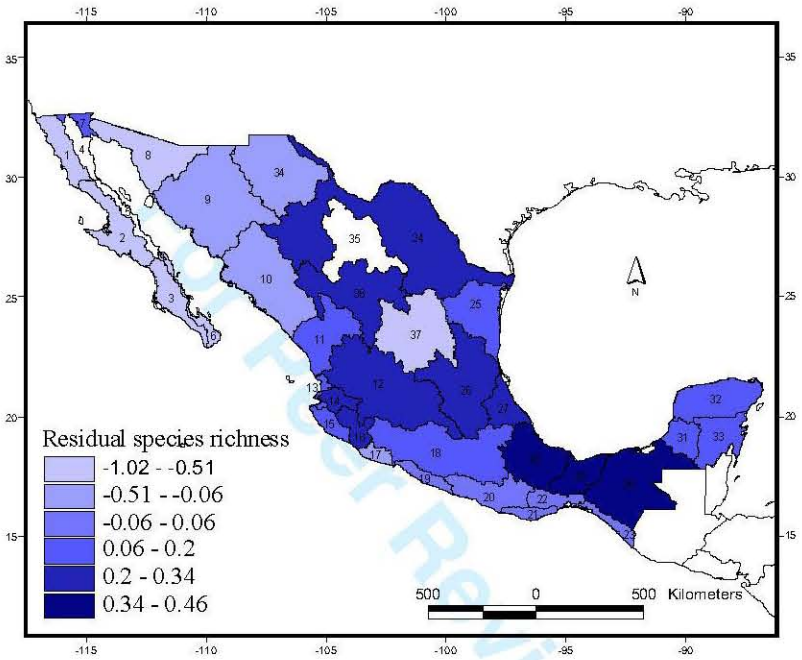
Figure 1 Distributional pattern of species richness of Mexican freshwater fishes at the hydrological region level.



1=Baja California Noroeste, 2=Baja California Centro Oeste, 3=Baja California Suroeste, 4=Baja California Noreste, 5= Baja California Centro Este, 6= Baja California Sureste, 7=Río Colorado, 8=Sonora Norte, 9=Sonora Sur, 10=Sinaloa, 11=Presidio-San Pedro, 12=Lerma-Santiago, 13=Huicicila, 14=Río Ameca, 15=Costa de Jalisco, 16=Armería-Coahuayana, 17=Costa de Michoacán, 18=Balsas, 19=Costa Grande de Guerrero, 20=Costa Chica de Guerrero, 21=Costa de Oaxaca, 22=Tehuantepec, 23=Costa de Chiapas, 24=Bravo-Conchos, 25= San Fernando-Soto La Marina, 26=Pánuco, 27=Norte de Veracruz, 28=Papaloapan, 29=Coatzacoalcos, 30=Grijalva-Usumacinta, 31=Yucatán Oeste, 32=Yucatán Norte, 33=Yucatán Este, 34=Cuencas Cerradas del Norte, 35=Mapimí, 36=Nazas-Aguanaval, 37=El Salado.

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Figure 2 The frequency distributions of body sizes for Mexican freshwater fishes. (a) arithmetic and (b) logarithmic scale classes.

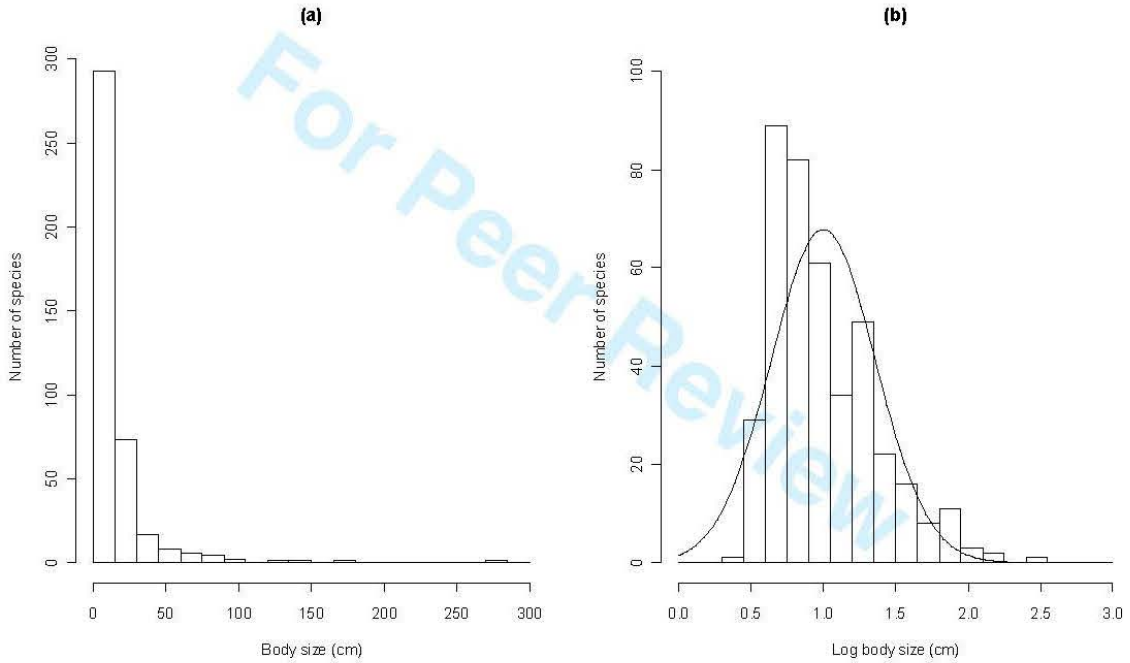

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Figure 3 The frequency distributions of geographical range sizes for Mexican freshwater fishes, with arithmetic (a-e) and logarithmic (f-j) scale classes.

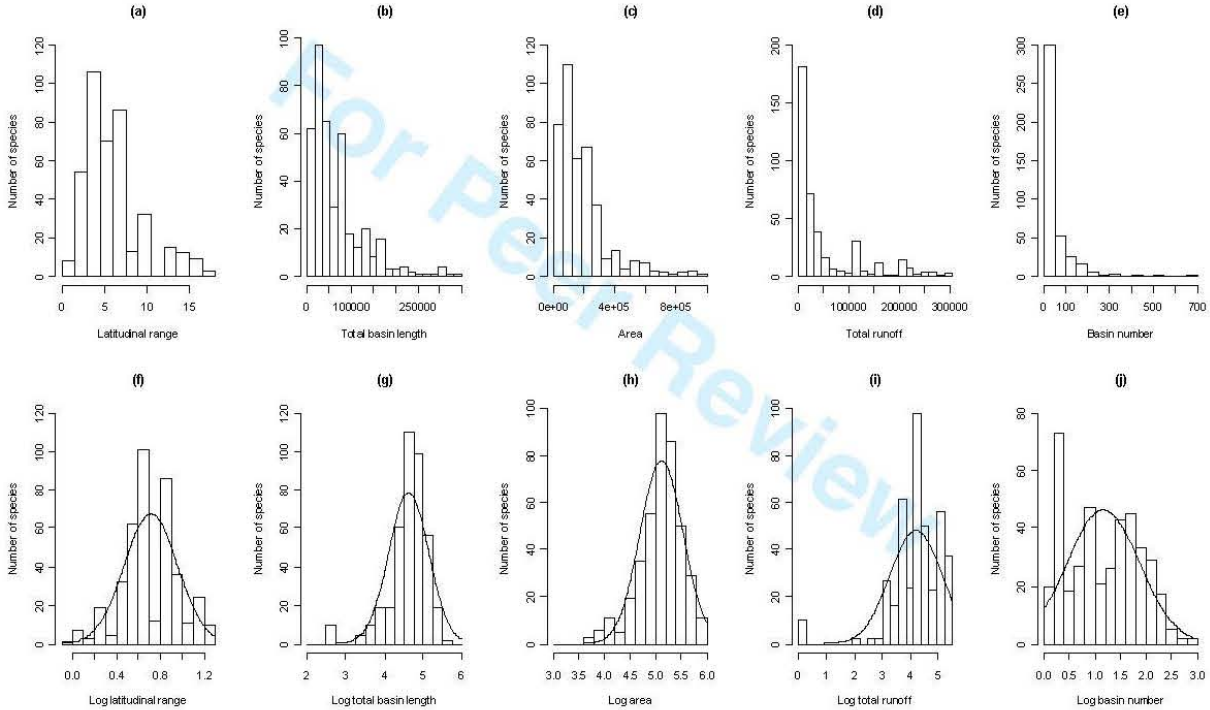

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Figure 4 Relationships between latitude and (a) body sizes and (b-f) geographical range sizes for Mexican freshwater fishes.

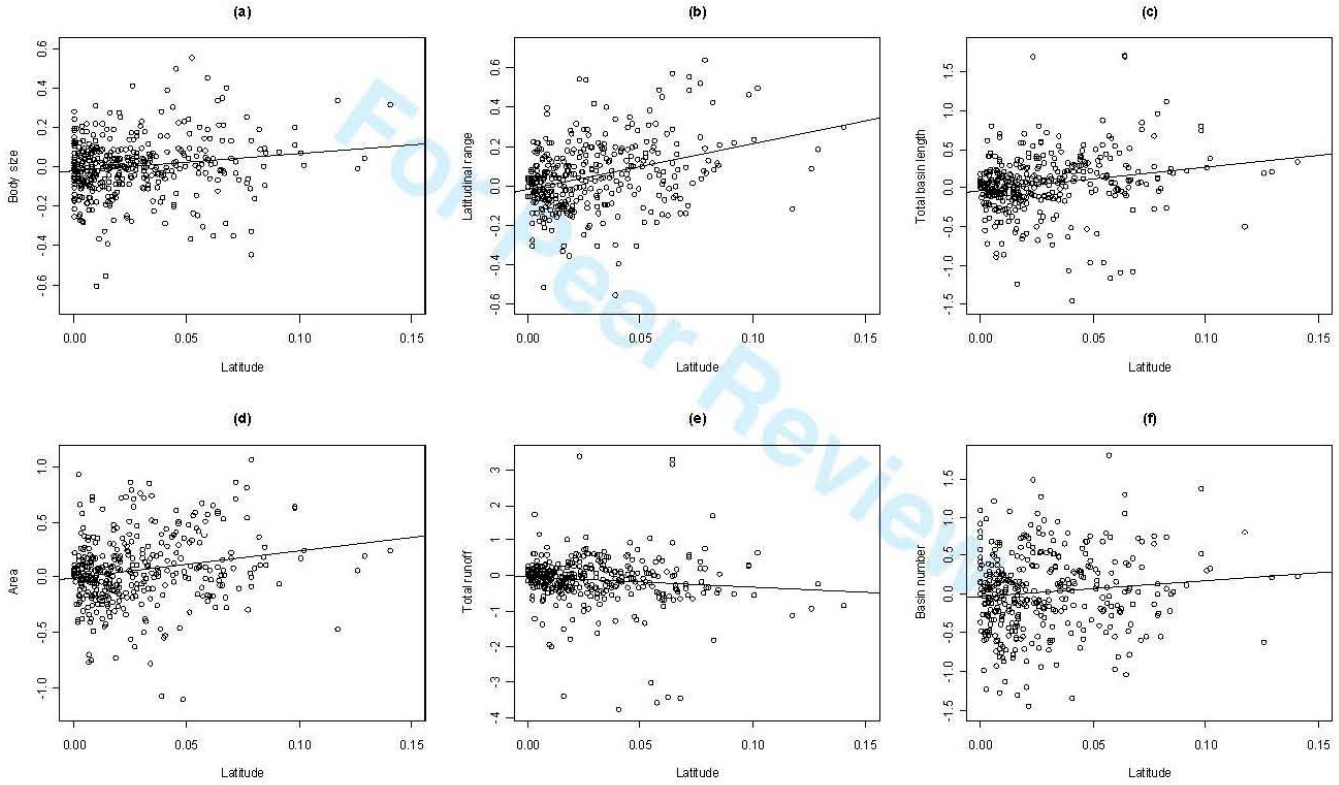

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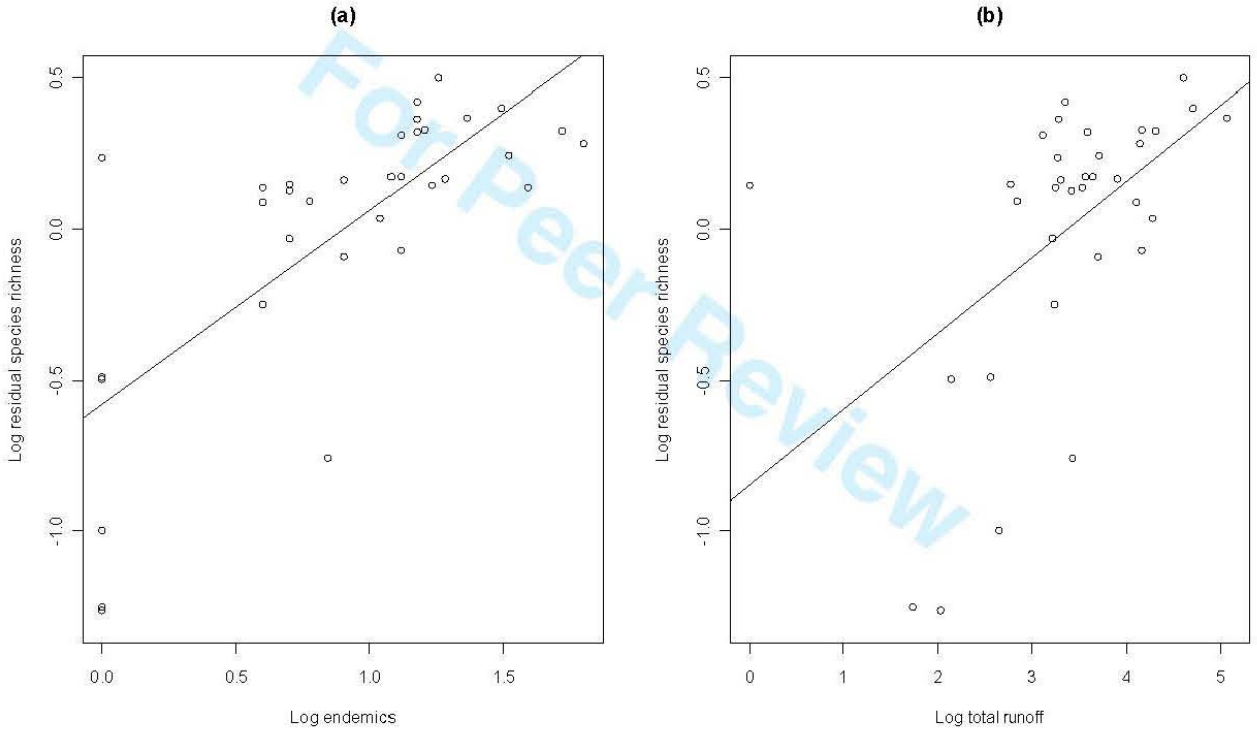
Figure 5 Residual species richness of Mexican freshwater fishes for each hydrological region as a function of history and area-related variables.



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SUPPORTING INFORMATION

Appendix S1 Figures show the composite phylogeny of the native Mexican freshwater fish species, where the asterisks identify taxa recorded only in Mexico. The phylogenetic relationships at the order level were based on Nelson (2006), while in other taxonomic levels it was constructed from hypothesis generated mainly through molecular studies (Rauchenberger, 1989; Meyer *et al.*, 1994; Ptacek & Breden, 1998; Perdices *et al.*, 2002; Reznick *et al.*, 2002; Schönhuth & Doadrio, 2003; Simons *et al.*, 2003; Doadrio & Dominguez, 2004; Webb *et al.*, 2004; Wilcox *et al.*, 2004; Near *et al.*, 2005; Hulsey *et al.*, 2006; Concheiro Pérez *et al.*, 2007; Hrbek *et al.*, 2007; Lang & Mayden, 2007; Hardman & Hardman, 2008; Hertwig, 2008; Rícan *et al.*, 2008; Bloom *et al.*, 2009, 2012; Mirande, 2009; Pérez-Rodríguez *et al.*, 2009; Doosey *et al.*, 2010; McMahan *et al.*, 2010; Schönhuth & Mayden, 2010; Martin & Wainwright, 2011; Schönhuth *et al.*, 2012).

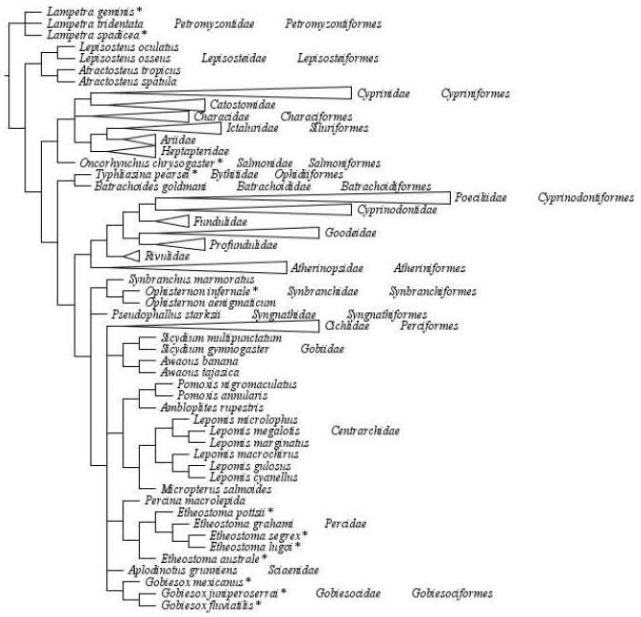

Figure S1 Phylogenetic relationships among Mexican freshwater fish orders.

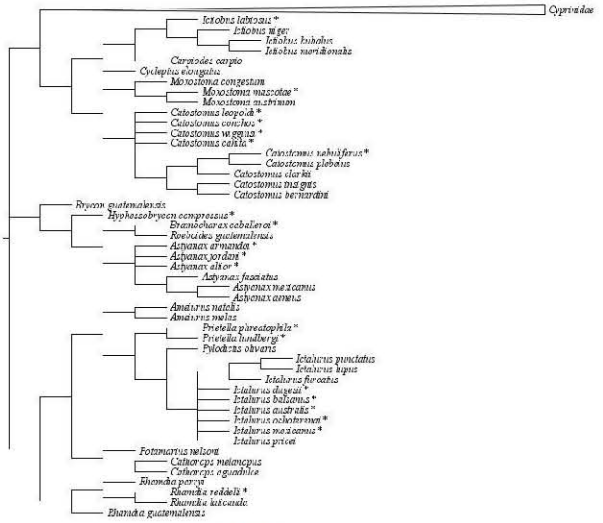

Figure S2 Phylogenetic relationships within the Cypriniformes, Characiformes and Siluriformes orders.

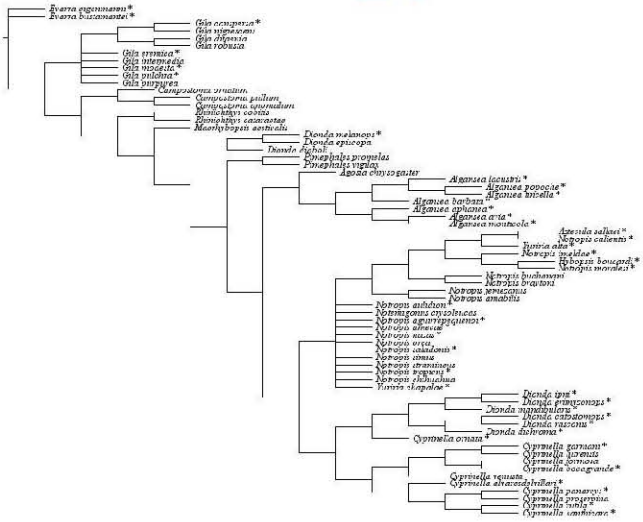

Figure S3 Phylogenetic relationships among species of the Cyprinidae family.

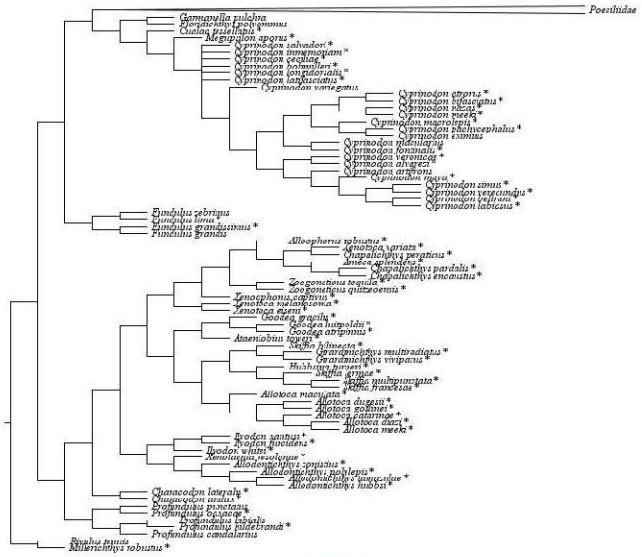

Figure S4 Phylogenetic relationships within the Cyprinodontiformes order.

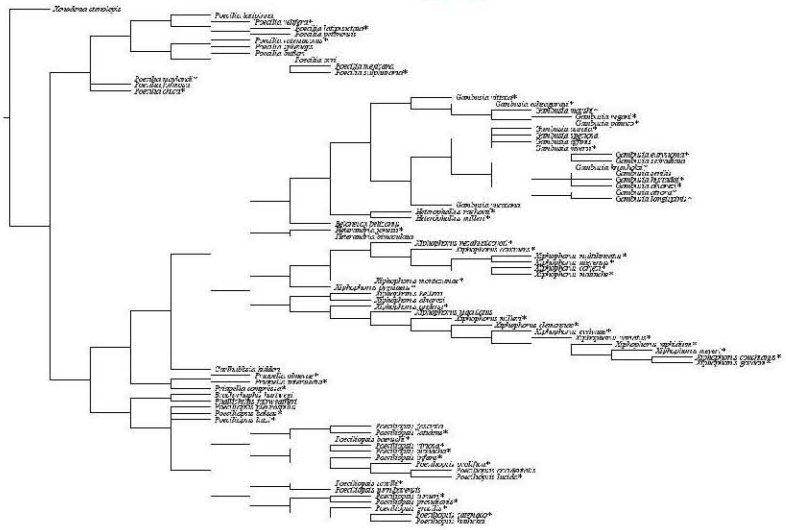

Figure S5 Phylogenetic relationships among species of the Poeciliidae family.

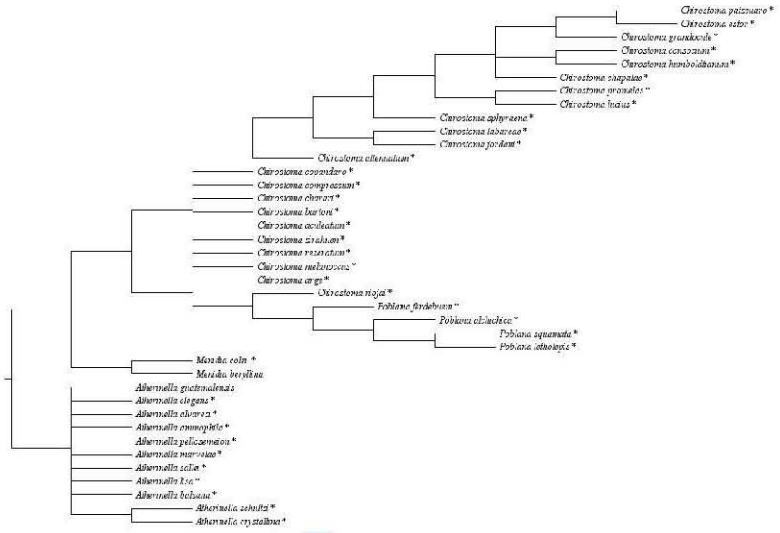

Figure S6 Phylogenetic relationships among species of the Atherinopsidae family.

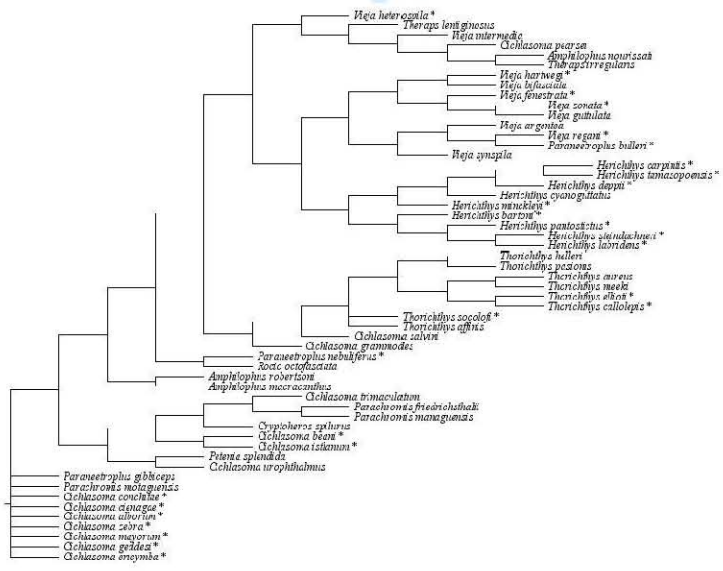

Figure S7 Phylogenetic relationships among species of Cichlidae family.

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CAPÍTULO II

The influence of host ecology and biogeography on the helminth species richness of freshwater fishes in Mexico

L. GARRIDO-OLVERA[1], H. T. ARITA[2] *and* G. PÉREZ-PONCE DE LEÓN[3]*

[1] *Posgrado en Ciencias Biológicas, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Apartado Postal 70-275, C. P. 04510, Distrito Federal, México*
[2] *Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro 8701, Ex-Hacienda de San José de La Huerta, C. P. 58190, Morelia, Michoacán, México*
[3] *Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Apartado Postal 70-153, C. P. 04510, Distrito Federal, México*

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SUMMARY

Freshwater fish helminths, the most well known Mexican vertebrate parasites, include approximately 260 species (platyhelminthes, acanthocephalans, nematodes, and hirudineans). The distribution patterns of adult helminth diversity (throughout parasite and host groups and hydrological regions) are described and the effects of host traits and environmental and geographical factors on diversity are evaluated. Adult helminths include 160 species, parasitizing 149 fish species of 23 families distributed in 21 regions. Nematoda was the most species-rich (> 50 species). Cichlidae harboured rich helminth assemblages, with widespread parasites. By contrast, Atherinopsidae and Goodeidae showed relatively poor helminth assemblages, including specific parasites with narrow distribution. Helminth richness in southeastern Mexico was higher than northern or central regions. Non-parametric richness estimators were used to avoid confusion in comparisons with unequal sampling efforts. Bootstrap values, the method with the best performance, indicated that estimated richness shows the same distribution pattern that observed richness. Non-phylogenetic and phylogenetic analyses were used to determine the role of different factors in the parasite diversification. The distribution range was the most important richness predictor (widespread fishes harbour richer parasite assemblages), although interactions between this variable and others such as trophic level, latitude, habitat temperature and precipitation are also important. Likewise, biogeographical factors can also affect parasite diversity.

Key words: geographical range, parasites, diversity, independent contrasts, Nearctic region, Neotropical region, hydrological regions, Osteichthyes.

INTRODUCTION

The evolutionary events determining the structure of a parasite assemblage are relatively well understood. A parasite species may have been inherited by the host species from its ancestor, may be the result of an intra-host speciation event, and/or may have colonized the host species from another sympatric host species (host switching) (Paterson and Gray, 1997). Therefore, it is possible to search for the key factors that have caused certain parasite assemblages to diversify more than others over evolutionary time (Poulin, 1998*a*; Page, 2003). The studies attempting to determine which host features may promote the diversification of parasite assemblages are based on 2 theoretical frameworks. First, following island biogeography theory (MacArthur and Wilson, 1967; Kuris *et al.* 1980), host features that promote high rates of parasite speciation or colonization, and low probabilities of extinction, by parasite species should be associated with high parasite diversity (e.g. large body size, broad geographical range, breadth of habitats). Epidemiological modelling represents the second theoretical source of predictions regarding parasite diversity (Dobson and Roberts, 1994; Roberts *et al.* 2002). These models suggest that host population density, which regulates the contact rate between parasite infective stages and hosts, is the key factor determining whether a parasite species can invade and persist in a host population. Comparing different host species, those occurring at higher population density (e.g. schooling fish species) should harbour more species of parasites, because they exceed the persistence threshold of more parasite species than hosts with low population density.

Several studies have investigated the factors potentially controlling the number of parasite species in freshwater and marine fishes (Bell and Burt, 1991; Guégan and Kennedy, 1993; Poulin, 1995; Poulin and Rohde, 1997; Sasal *et al.* 1997; Morand *et al.* 2000; Luque and Poulin, 2004, 2008). However, the

* Corresponding author: Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Apartado Postal 70-153, C. P. 04510, Distrito Federal, México. Tel: +56229131. Fax: +55500164. E-mail: ppdleon@ibunam2.ibiologia.unam.mx

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results available to date show very little consistency, since some studies claim that a certain variable is a predictor of parasite species richness, either host body size, host geographical range, host diet, etc., but no consensus on a particular variable as the main determinant has been reached.

Freshwater fish helminths are undoubtedly the most well known group of vertebrate parasites in Mexico, because fishes have been studied more than any other group (Pérez-Ponce de León and Choudhury, 2010; Pérez-Ponce de León *et al.* 2011). The helminth fauna of these hosts includes approximately 260 species (Oceguera-Figueroa *et al.* 2010; Pérez-Ponce de León and Choudhury, 2010). The first descriptions of distributional patterns of fish-parasite and drainage associations indicated that the parasite fauna is largely circumscribed by higher levels of monophyletic host taxa, especially at the level of fish family. Likewise, areas within a certain biogeographical region and consequently with similar fish composition possess more similar parasite faunas compared to areas with less similar fish faunal composition (Pérez-Ponce de León and Choudhury, 2005). Recently, Pérez-Ponce de León and Choudhury (2010) evaluated the progress made on the inventory of freshwater fish helminths of Mexico and suggested that following a traditional approach, the inventory is nearing completion for most helminth groups (except monogeneans). These authors suggested that host species and geographical areas that would be targeted in the future could be expected, with very few exceptions, to have helminth faunas that are consistent with the fish composition in those areas. However, they argued that in the future DNA-based taxonomic methods have the potential to alter drastically the estimates of helminth diversity in freshwater fishes, because of the existence of cryptic species (morphologically indistinguishable but genetically distinct, see Poulin, 2011; Nadler and Pérez-Ponce de León, 2011) in several lineages of helminths in Mexico. Despite this fact, they described species richness patterns and pointed out that the diversity is distributed heterogeneously. These patterns were described by considering all freshwater helminth parasites irrespective of their developmental stage i.e. larval and adult forms, under a strict definition of what constitutes a freshwater species and by including both native and introduced fish species. However, Pérez-Ponce de León and Choudhury (2010) did not use the proper methods to analyse data with unequal sampling effort that might act as a confounding factor. In addition, potential factors that cause the heterogeneous distribution of helminth species richness were not explored. For these reasons, our aims in this paper are to describe the distribution patterns of adult helminth diversity throughout parasite and host groups as well as across hydrological regions, and to investigate the host traits and/or environmental and geographical factors that determine the uneven diversification of assemblages of freshwater fish helminths.

MATERIALS AND METHODS

A database updated to November, 2011, with distribution records for Mexican freshwater fish helminths (trematodes, monogeneans, cestodes, acanthocephalans, nematodes, and hirudineans) was constructed. Our study was restricted to adult helminths of the native freshwater fishes, which are unable to disperse across brackish and marine waters (i.e., presumably non-diadromous). Larval helminths were excluded because of the confounding effects of dispersal caused by their definitive hosts in any distribution pattern. Also, if we consider larval stages, the parasite species count could be underestimated because they often cannot be identified to the species level and one putative taxon might actually consist of more than one species.

The data set was mostly obtained from monographs (e.g. Pérez-Ponce de León *et al.* 1996, 2007; Garrido-Olvera *et al.* 2006; Kohn *et al.* 2006; Salgado-Maldonado, 2006; García-Prieto *et al.* 2010; Oceguera-Figueroa *et al.* 2010) and specimens deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. Nomenclature was updated using specialized literature (e.g. Scholz *et al.* 1997; Moravec, 1998; Scholz *et al.* 2001; Vidal-Martínez *et al.* 2001; Aguirre-Macedo and Scholz, 2005; Caspeta-Mandujano, 2005; Pérez-Ponce de León *et al.* 2007). To avoid cases of synonymies among fish species, valid species names were adopted according to FishBase (Froese and Pauly, 2011).

The geographical distribution patterns were recognized through distribution maps for each taxon, which were prepared using ArcView GIS 3.2 (ESRI, 1999). Sample-based rarefaction curves considering the number of localities studied as a measure of sampling effort were used to compare the helminth species richness (the number of parasite species in an assemblage) between host families and hydrological regions at comparable sampling effort (Colwell *et al.* 2004). Non-parametric species richness estimators are also used to analyse data with unequal sampling effort. Therefore, total helminth species richness for each data set was calculated using 5 estimation methods: ICE, Chao2, Jackknife1, Jacknife2, and Bootstrap (Poulin, 1998*b*; Walther and Morand, 1998). In addition, an evaluation of the performance of these estimators with the unscaled measures of bias, precision, and accuracy was conducted (Walther and Moore, 2005). EstimateS version 8.2 was used to obtain rarefaction curves and total species richness (Colwell, 2006).

In order to examine the possible factors determining the helminth species richness in an assemblage,

we gathered detailed information on the fish species and geographical areas. The host traits were obtained from Miller *et al.* (2005) and Froese and Pauly (2011) (Table 1). The environmental and geographical data for each hydrological region were obtained from the Comisión Nacional del Agua (2008) and Fernandez-Eguiarte *et al.* (2010) (Table 2).

The helminths include various taxonomic groups, with different biological characteristics related with life-cycle dynamics and transmission modes. Therefore, these parasite taxa may be subjected to different factors potentially influencing their species richness. For this reason, helminth species richness for each assemblage was estimated in 3 ways: for all parasites, for endoparasites only (trematodes, cestodes, acanthocephalans, and nematodes), and for ectoparasites only (monogeneans and hirudineans).

To analyse factors influencing differences in species richness among assemblages, the information on the fish species and their distribution regions was combined. In the initial analyses, fish species were treated as independent observations. The relationships between helminth species richness and continuous variables were tested through correlations, while the influence of categorical variables was assessed by inspecting mean values. Next, we determined which factors played a role in the diversification of parasite assemblages, i.e., we tested whether any of those associations were significant and whether there were interactions between the explanatory variables by performing generalized linear models, where species richness (total parasites, ectoparasites, and endoparasites, independently) was the response variable and host traits were explanatory variables. The models were fitted with a log link (to ensure that the fitted values are bounded below) and Poisson errors (to account for the non-normality) (Crawley, 2007).

Parasite assemblages of closely related host species are not truly independent statistical observations. Therefore, we used Felsenstein's (1985) comparative method to control for the effects of phylogenetic association between host species. The PDAP: PDTREE software (Midford *et al.* 2011), implemented in Mesquite Modular System for Evolutionary Analysis, Mesquite version 1.12 (Maddison and Maddison, 2011) was used to compute independent contrasts. Host phylogeny was constructed from mainly molecular studies and the phylogenetic relationships of the orders were based on Nelson (2006), as follows: ((((((*Ophisternon aenigmaticum*, (*Eugerres mexicanus, Etheostoma* sp., ((*Lepomis megalotis, L. macrochirus*), *Micropterus salmoides*), *Aplodinotus grunniens, (Awaous banana, Sicydium multipunctatum*), (*Cichlasoma geddesi, C. mayorum*, (((*C. beani, C. istlanum*), ((*Parachromis friedrichsthalii, C. trimaculatum*), (*Petenia splendida, C. urophthalmus*))), ((*Rocio octofasciata, Amphilophus robertsoni*), ((*C. salvini*, ((*Thorichthys helleri, T. pasionis*), (*T. meeki*, (*T. ellioti, T. callolepis*))))), ((*Herichthys labridens*, (*H. minckleyi, H. cyanoguttatus*)), ((*C. pearsei*, (*Theraps lentiginosus, Vieja intermedia*)), ((*V. fenestrata*, (*V. bifasciata, V. hartwegi*)), (*V. synspila, V. argentea*)))))))))), ((((((*Cyprinodon meeki, C. nazas*), ((((*Poecilia butleri, P. mexicana*), (*P. sphenops, P. catemaconis*)), (*P. velifera*, (*P. petenensis, P. latipunctata*))), (((*Poeciliopsis catemaco, P. gracilis*), (*P. infans, P. baenschi*), *P. balsas*), ((*Xiphophorus hellerii, X. variatus*), (*Heterandria bimaculata, (Belonesox belizanus*, ((*Gambusia vittata, G. marshi*), *G. senilis, G. yucatana*))))))), ((*Profundulus hildebrandi, P. punctatus, P. labialis*), ((*Characodon audax, C. lateralis*), (((*Ilyodon cortesae, I. whitei, I. furcidens*), (*Xenotaenia resolanae*, ((*Allodontichthys tamazulae, A. hubbsi*), *A. zonistius*))), (((((((*Chapalichthys encaustus, C. pardalis*), *Ameca splendens*), *Xenotoca variata*), *Alloophorus robustus*), *Zoogoneticus quitzeoensis*), (*X. eiseni, X. melanosoma*)), ((*Ataeniobius toweri*, (*Goodea atripinnis , G. gracilis*)), (((*Girardinichthys multiradiatus, G. viviparus*), (*Hubbsina turneri*, (*Skiffia bilineata, S. multipunctata, S. lermae*))), (((((*Allotoca catarinae*, (*A. diazi, A. meeki*)), *A. zacapuensis*), *A. dugesii*), *A. maculata*), *A. regalis*)))))))), (*Strongylura* sp., *Hyporhamphus mexicanus*)), ((*Atherinella crystallina, A. balsana*), (((((*Poblana letholepis, P. squamata*), *P. alchichica*), *Chirostoma riojai*), *Ch. arge*), (*Ch. attenuatum*, ((*Ch. jordani, Ch. labarcae*), (*Ch. lucius*, (*Ch. humboldtianum*, (*Ch. grandocule, Ch. estor*))))))))), *Typhliasina pearsei*), (((*Rhamdia guatemalensis*, (*Potamarius nelsoni*, (*Ameiurus melas*, (*Pylodictis olivaris*, ((*Ictalurus furcatus, I. punctatus*), *I. balsanus, I. mexicanus, I. pricei, I. dugesii*))))), ((*Ictiobus meridionalis, Catostomus nebuliferus*), ((((*Algansea lacustris, A. tincella*), *A. monticola*), *Gila conspersa*), (*Campostoma ornatum*, (*Dionda ipni*, (*Pimephales promelas*, (((((*Notropis calientis, Aztecula sallaei*), *Yuriria alta*), *Hybopsis boucardi*), *N. nazas, N. chihuahua*), (*Codoma ornata*, ((*Cyprinella garmani, C. lutrensis*), *C. xanthicara*)))))))), ((((*Astyanax aeneus, A. mexicanus*), *A. fasciatus*), *Bramocharax caballeroi*), *Brycon guatemalensis*)), ((*Dorosoma cepedianum, D. petenense*), *D. anale*))), *Atractosteus tropicus*); (Ptacek and Breden, 1998; Breden *et al.* 1999; Harris and Mayden, 2001; Reznick *et al.* 2002 ; Miya *et al.* 2003; Schönhuth and Doadrio 2003; Simons *et al.* 2003; Cunha *et al.* 2002; Doadrio and Dominguez, 2004; Wilcox *et al.* 2004; Near *et al.* 2005; Hulsey *et al.* 2006; Chakrabarty, 2007; Concheiro Pérez *et al.* 2007; Hrbek *et al.* 2007; Hardman and Hardman, 2008; Hertwig, 2008; Lavoué *et al.* 2008; Rícan *et al.* 2008; Bloom *et al.* 2009, 2012; Mirande 2009; Pérez-Rodríguez *et al.* 2009; McMahan *et al.* 2010; Schönhuth and Mayden, 2010).

True branch lengths are not available in this tree, so all branch lengths were set to unity, which adequately standardized contrasts of all variables.

Table 1. Summary information to family level of freshwater fish species recorded as hosts of adult helminths in Mexico

(The number of fish species was obtained from Miller *et al.* (2005) and Froese and Pauly (2011).)

Family	Fishes	Helminths	Size ± S.D.	Regions	Environment	Geographical range	Trophic level ± S.D.	Climate
Ariidae*	3/1	4/-, 1, 3	39	1	D	M	3·58	Tr
Atherinopsidae	39/14	10/12, 2, 8	13·91 ± 9·53	4	B, P	M	3·06 ± 0·15	Tr
Belonidae*	4/1	4/-, -, 4	49·8	1	P	MCA	4·13	Tr
Bythitidae*	1/1	1/-, -, 1	9·7	1	D	M	3·3	Tr
Catostomidae	18/2	8/10, -, 8	39·95 ± 34·72	4	P, D	M, MCA	2·94 ± 0·24	Tr
Centrarchidae	10/3	16/21, 8, 8	37·67	5	B	MNA	3·55	S, Tm
Characidae	10/5	28/34, 9, 19	17·26 ± 13·46	11	B	M, MSA, MCA, MNA	2·81 ± 0·34	S, Tr
Cichlidae	55/27	58/69, 12, 44	18·56 ± 7·07	12	B, D	M, MCA, MNA	3·12 ± 0·73	S, Tr
Clupeidae	11/3	9/11, 2, 7	26·13 ± 8·52	3	P, PN	MCA, MNA, NAMCA	2·96 ± 0·51	Tr, S
Cyprinidae	69/23	14/17, 4, 10	10·02 ± 6·26	7	B, D	M, MNA	2·815 ± 0·27	S, Tm, Tr
Cyprinodontidae	28/2	5/6, 1, 4	4·75 ± 0·21	2	B	M	2·94 ± 0	Tr
Gerreidae*	11/1	3/-, 2, 1	20·8	2	D	MCA	3·35	Tr
Gobiidae*	4/2	3/-, -, 3	21·5	3	B, D	NAMCASA	2·025	Tr
Goodeidae	41/33	24/28, 5, 19	7·72 ± 3·01	7	B, D, P	M	2·09 ± 0·17	S, Tm, Tr
Hemiramphidae*	4/1	1/-, -, 1	16·1	1	P	MCA	3·02	Tr
Heptapteridae	4/1	24/28, 6, 18	30 ± NA	4	B	MSA	3·16 ± NA	Tr
Ictaluridae	14/8	35/40, 7, 28	67·23 ± 26·99	13	B, D	M, MNA, NAMCA	3·63 ± 0·15	S, Tm, Tr
Lepisosteidae	4/1	6/7, 1, 5	85·9 ± NA	2	D	MCA	4·23 ± NA	Tr
Percidae*	6/1	1/-, 1, -	5	1	B	M	3·17	Tr
Poeciliidae	82/20	22/26, 5, 17	7·55 ± 3·28	12	B, D	M, MCA, MSA, MNA	2·72 ± 0·48	S, Tr
Profundulidae*	5/3	4/-, -, 4	10·4	2	B	MCA	3·073	Tr
Sciaenidae*	1/1	5/-, 3, 2	50	3	D	NAMCA	3·36	S
Synbranchidae*	3/1	7/-, -, 7	20·8	1	D	MCA	3·25	Tr

* Data were insufficient for estimating total parasite species richness. Fishes, total/known host fish species; Helminths, observed/estimated total species richness, ectoparasites, endoparasites; Size ± S.D., mean body size (standard length in cm) ± standard deviation; Regions, number of regions where fish family is distributed; Environment: B, Benthopelagic, D, Demersal, P, Pelagic, PN, Pelagic-neritic; Trophic level ± S.D. = mean trophic level ± standard deviation; Climate: S, subtropical, Tr, tropical, Tm, temperate; Geographical range: M, Mexico, MCA, Mexico and Central America, MNA, Mexico and North America, MSA, Mexico and South America, NAMCA, North America, Mexico and Central America, NAMCASA, North America, Mexico, Central America, and South America.

Table 2. Summary information on Mexican hydrological regions, where adult helminth species have been recorded as parasites of freshwater fishes

(The number of fish species is result of a review of databases of fish collections and fish lists of Miller *et al.* (2005) and Froese and Pauly (2011).)

Region	Fishes	Helminths	MxL	MnL	ML	Length	Area	Flow	Basins	MAP	PDM	PWM	MTWM	MTCM	Slope
9*	34/4	3/-, -, 3	31·33	26·6	28·97	39 635	139 370	4935	48	507·2	0·11	22·8	34·55	7·21	P
11	33/13	16/19·73, 2, 14	25·18	21·69	23·44	19 704	51 717	7956	9	815·2	7·36	215·91	32·88	5·88	P
12	74/41	36/44·03, 12, 24	23·42	19·06	21·24	51 096	132 916	13 637	8	723·2	0·37	81·02	34·33	9·51	P
14*	25/6	4/-, -, 4	21·28	20·07	20·68	6132	12 255	2236	1	122·7	4·34	92·2	32·49	3·21	P
15*	17/1	3/-, -, 3	20·45	18·88	19·67	6307	12 967	3684	45	1185·5	16·3	153·35	34·47	8·83	P
16	29/11	14/18·05, -, 14	20·45	18·59	19·52	7393	17 628	3882	8	911·3	7·28	71·58	30·69	4·16	P
18	54/27	33/40·01, 3, 30	19·99	17·02	18·51	45 372	118 268	1757	3	949·7	15·22	184·34	30·82	7·72	P
19*	16/1	1/-, -, 1	18·14	16·7	17·42	4992	12 132	691	41	1232	5·27	182·06	29·94	4·83	P
20*	24/3	4/-, 1, 3	17·62	15·98	16·8	12 907	39 936	18 714	21	1393·1	42·26	288·22	30·45	11·11	P
23*	17/1	1/-, -, 1	16·54	14·53	15·54	3908	12 293	12 554	25	2352·7	5·46	261·16	31·43	8·25	P
24	101/14	27/33·81, 7, 20	31·77	24·85	28·31	77 898	229 740	5156	2	448·5	2·82	318·3	33·27	13·73	A
25*	41/4	9/-, 4, 5	25·76	22·28	24·02	16 729	54 961	4328	27	758·5	4·27	224·06	31·37	10·11	A
26	77/21	24/28·74, 4, 20	23·95	19·04	21·5	34 263	96 989	20 329	2	889·2	34·07	200·23	33·66	16·87	A
27*	38/3	10/-, 1, 9	22·2	19·48	20·84	10 139	26 592	14 306	38	1423·2	4·08	216·68	32·42	10·13	A
28	67/23	49/58·6, 11, 38	19·74	16·93	18·34	19 382	57 355	49 951	31	1447·1	22·85	220·73	35·28	15·79	A
29*	52/19	28/-, 11, 17	18·44	16·63	17·54	8866	30 217	39 482	10	1953·8	28·39	344·94	30·99	12·36	A
30	86/37	61/71·03, 19, 42	18·9	15·3	17·1	23 249	102 465	117 546	4	1708·9	38·47	326·82	32·86	15·17	A
31*	32/7	12/-, 3, 9	19·97	17·81	18·89	1704	25 443	591	6	1227·4	2·78	272·12	31·39	12·94	A
32	42/15	40/45·98, 17, 23	21·61	19·63	20·62	523	58 135	0	1	192·4	45·93	424·76	33·66	16·71	A
33	37/10	19/22·31, 6, 13	20·1	17·81	18·96	2926	38 308	1989	2	1239·8	2·8	323·08	33·58	17·24	A
36	33/14	9/11·24, -, 9	26·6	22·67	24·64	31 046	9332	1912	1	422·1	7·3	457·02	34·1	16·7	I

* Data were insufficient for estimating total species richness. Region, 9, Sonora Sur; 11, Presidio-San Pedro; 12, Lerma-Santiago; 14, Río Ameca; 15, Costa de Jalisco; 16, Armería-Coahuayana; 18, Balsas; 19, Costa Grande de Guerrero; 20, Costa Chica de Guerrero; 23, Costa de Chiapas; 24, Bravo-Conchos; 25, San Fernando-Soto La Marina; 26, Pánuco; 27, Norte de Veracruz; 28, Papaloapan; 29, Coatzacoalcos; 30, Grijalva-Usumacinta; 31, Yucatán Oeste; 32, Yucatán Norte; 33, Yucatán Este; 36, Nazas-Aguanaval; Fishes, total/ known host fish species; Helminths, observed/estimated total species richness, ectoparasites, endoparasites; MxL, maximum latitude; MnL, minimum latitude; ML, mean latitude; Length, total length of rivers (in km); Area, area (in km^2); Flow, mean current flow (in hm3/year); Basins, basin number in the region; MAP, mean annual precipitation (mm); PDM, precipitation of driest month (mm); PWM, precipitation of wettest month (mm); MTWM, maximum temperature of warmest month (°C); MTCM, minimum temperature of coldest month (°C); Slope, A, Atlantic, I, Interior, P, Pacific.

The program can only compute independent contrasts in continuous variables. In order to obtain independent contrasts of categorical variables, we treated these variables as continuous with states of 1, 2, 3 or more as recommended by Midford *et al.* (2011) in the PDAP:PDTREE manual.

The relationships among independent contrasts were assessed using least-squares regressions forced through the origin (Garland *et al.* 1992). The possibility that multiple host traits influence parasite diversity was also addressed and then contrasts in independent variables (host traits) were entered into multiple regression methods (computed through the origin) to predict contrasts in species richness (total parasites, ectoparasites, and endoparasites, independently) (Crawley, 2007).

In both generalized linear models and multiple regression analyses, the minimal adequate models were obtained with categorical and continuous explanatory variables, separately (i.e., models without redundant parameters or factor levels). We achieved this by fitting a maximal model and then simplifying it by stepwise deletion: non-significant terms were left out, and significant terms were added back (Crawley, 2007). All statistical analyses were conducted in the software R version 2.11.0 for Windows (http://www.r-project.org/).

RESULTS

The adult helminth fauna parasitizing freshwater fishes in Mexico is composed by 160 species belonging to 6 groups. The most numerous group was Nematoda with more than 50 species, followed by Trematoda and Monogenea, with 39 species each. The remaining groups were composed by no more than 10 species each (4 Hirudinea, 6 Acanthocephala, and 9 Cestoda). No parasite species occurred in all hydrological regions, but the cestode *Bothriocephalus acheilognathi* and the acanthocephalan *Neoechinorhynchus golvani* were distributed in 14 and 11 regions, respectively. In contrast, more than 100 species (approximately 60% of total parasite species) were recorded from only 1 region. The most generalist helminth species were the cestode *B. acheilognathi* and the nematode *Rhabdochona kidderi* parasitizing 11 and 10 host families, respectively. However, approximately 120 species (75% of total parasite species) infected only 1 fish family each.

In total, 149 fish species belonging to 23 families have been recorded as hosts of adult helminths. This means that approximately 40% of Mexican freshwater fishes have been recorded as hosts of these parasites. Helminths were found infecting 8% to 100% of the species included in each host family, though the highest percentages correspond to monotypical families. With the exception of the Cyprinodontidae and Catostomidae, the more species-rich host groups (i.e., Poeciliidae, Cyprinidae, Cichlidae, Goodeidae, Atherinopsidae, and Ictaluridae, which account for more than 80% of the Mexican ichthyofauna) have been sampled with relatively high intensity, since at least 24%, 33%, 49%, 81%, 36%, and 57%, of their species, respectively, have been recorded as hosts of helminths (Table 1).

In terms of geographical distribution, freshwater fish adult helminths were found in 198 localities pertaining to 21 of the 37 Mexican hydrological regions. The number of records was reduced in most of the regions located in the Nearctic biogeographical region and in coastal areas. In contrast, Lerma-Santiago, Balsas, Grijalva-Usumacinta, Nazas-Aguanaval, and Presidio-San Pedro were the best known hydrological regions, considering the number of fish species recorded as hosts and the actual number of fish species occurring in each region as well as the number of localities studied (Fig. 1, Table 2).

Although the sample-based rarefaction curves did not reach the asymptote, the majority showed a certain stability indicating that the sample size in each data set was large enough to consider that their adult helminth fauna was properly known. The comparisons of rarefaction curves at comparable sampling effort indicated that the difference in helminth species richness was significant among both host families and hydrological regions. The cichlids and ictalurids harboured the highest helminth species richness, whereas an intermediate number of species parasitized characids, goodeids, heptapterids, and poeciliids. The remaining host families did not harbour helminth faunas with more than 10 species (rarefaction curves not shown). At the species level, most fish species (60%) harboured poor helminth faunas (i.e., fewer than 5 species per host species). In contrast, only 6% of the fish species were parasitized by helminth faunas comprising more than 10 parasite species. The parasite species richness among hydrological regions also varied significantly. In southeastern Mexico, particularly in the Grijalva-Usumacinta and Papaloapan river basins, the highest helminth species richness was found. In contrast, with the exception of the regions situated in the Yucatán Peninsula, the hydrological regions with intermediate or low helminth species richness were always located in northern and central areas of the country (e.g. the Balsas, Lerma-Santiago, Nazas-Aguanaval and Pánuco systems) (rarefaction curves not shown).

We only considered the estimations of species richness produced by the bootstrap method, which achieved the best performance measures in all data sets. Based on these values, the minimum number of missing species remaining to be found varies from 1 to 11 and from 2 to 10 in the 13 host families and 11 hydrological regions analysed, respectively. Interestingly, the estimated species richness was distributed in the same way as the observed species

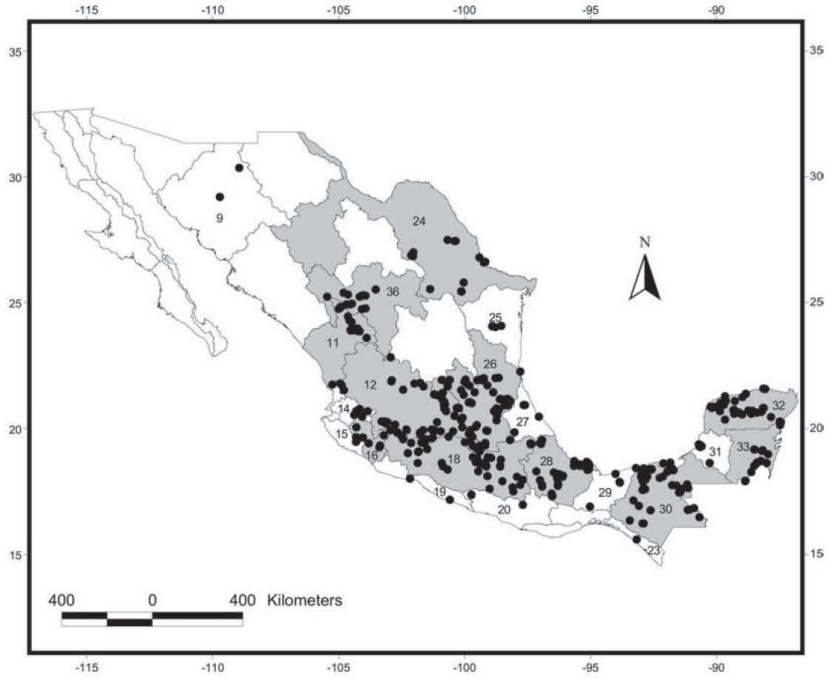

Fig. 1. Distribution of adult helminth parasites of freshwater fishes in Mexico. The country is divided in 37 hydrological regions and numbers indicate the regions where data are available: 9, Sonora Sur; **11**, Presidio-San Pedro; 12, Lerma-Santiago; 14, Río Ameca; 15, Costa de Jalisco; 16, Armería-Coahuayana; 18, Balsas; 19, Costa Grande de Guerrero; 20, Costa Chica de Guerrero; 23, Costa de Chiapas; 24, Bravo-Conchos; 25, San Fernando-Soto La Marina; 26, Pánuco; 27, Norte de Veracruz; 28, Papaloapan; 29, Coatzacoalcos; 30, Grijalva-Usumacinta; 31, Yucatán Oeste; 32, Yucatán Norte; 33, Yucatán Este; 36, Nazas-Aguanaval. Shaded regions are those for which the data were sufficient for comparative analysis.

richness in both host families and hydrological regions (Tables 1 and 2).

The analyses across fish species values, not corrected for possible phylogenetic effects, revealed that the extent of their geographical distribution correlated positively with species richness of ectoparasites, endoparasites, and total parasites. The r values obtained by considering the number of sites as well as the regions in which a host species occurs (within its regional distribution range) were 0·73 and 0·77, 0·78 and 0·70, and 0·83 and 0·78, $N=149$, $P=<2{\cdot}2\text{e-}16$, respectively. In addition, the total area of hydrological regions where fishes are distributed correlated positively with ectoparasite species richness ($r=0{\cdot}70$, $N=149$, $P=<2{\cdot}2\text{e-}16$). Based on main effect means of categorical variables, we also found that the distribution range of the host is an important variable and it seems that neotropical fishes have higher parasite species richness than those occurring in nearctic ones (Table 3).

In the generalized linear models performed on fish species values, only the following variables, geographical distribution, trophic level, temperature, precipitation and latitude were retained, with the distribution range being the most important explanatory variable. The aforementioned trend is significant and there is compelling evidence that fish species with a broad distribution range tend to harbour more parasite species. In addition, these models showed significant interactions between distribution range and temperature and between latitude and precipitation in determining the number of endoparasites (Table 4).

After controlling for phylogenetic influences by using the independent contrasts method (Felsenstein, 1985), the same factors (the number of sites and regions in which a host species occurs) were correlated with the helminth species richness (ectoparasites $r=0{\cdot}66$ and 0·74, endoparasites $r=0{\cdot}74$ and 0·65, and total parasites 0·79 and 0·74, respectively, $N=148$, $P=<2{\cdot}2\text{e-}16$).

The results of the regression analyses corroborated that the geographical range was a key determinant of the variability in parasite species richness among host species (Figs 2–4). These findings suggest that, on average, widespread fish species harbour more species

Table 3. Main effect means of categorical variables on helminth richness

(See Tables 1 and 2 for details of variables.)

Variable	Level	Ectoparasites	Endoparasites	Total parasites
Environment	B	2·10	4·67	6·77
	D	1·65	4·46	6·10
	P	1·38	3·25	4·63
	PN	2	3·5	5·5
Geographical range	M	1·51	3·72	5·23
	MCA	2·5	5·62	8·12
	MNA	2·07	4·47	6·53
	MSA	6	12·67	18·67
	NAMCA	3·33	9·33	12·67
Climate	S	2·65	5·96	8·61
	Tm	1·43	2·71	4·14
	Tr	1·80	4·34	6·13
Slope	A	2·14	4·93	7·07
	AI	3	8	11
	AP	3·56	6·94	10·50
	I	1	2·4	3·4
	IP	1	4·2	5·2
	P	1·33	3·52	4·85
	PIA	2	4	6

of helminth parasites and that this pattern is explained mainly by recent processes. Although, some results were similar when phylogenetic relationships were considered, there were some changes in the relationships between helminth species richness and their explanatory variables. For example, trophic level and latitude were not important in determining the number of endoparasites. In addition, a difference in parasite species richness between fish species with larger *vs* smaller body size was detected when data were corrected for host phylogeny (Table 4).

DISCUSSION

In this paper, we only considered adult helminth species found in native Mexican freshwater fishes unable to disperse across the sea (i.e., presumably non-diadromous), because of the fact that the parasite fauna of exotic fishes is not necessarily one they have acquired over evolutionary time in their area of origin. The species count provided in this study for adult helminths parasitizing freshwater fishes in Mexico (160) is not in agreement with species counts presented in previous studies. Part of the problem is the challenge in defining what is a freshwater fish (Miller *et al*. 2005). Salgado-Maldonado (2006) quantified approximately 180 adult parasite species of freshwater fishes, but this author listed some helminth species found in marine or brackish water fishes that regularly enter freshwater at some life-history stage. In a recent publication, after a detailed consideration of the status of the freshwater fish fauna where objective criteria were followed, Pérez-Ponce de León and Choudhury (2010) considered that the adult helminth fauna of freshwater fish in Mexico consists of 177 species (37 trematodes, 62 monogeneans, 15 cestodes, 6 acanthocephalans, and 54 nematodes); however, they considered both native and exotic species of fishes. In this context, the inclusion of either marine and brackish water fish species or exotic species could obscure not only any biodiversity pattern, but also biogeographical patterns, since the processes that determine the distribution of parasites are different in the sea than in freshwater.

An obvious pattern uncovered in this study after the analysis of the information is the asymmetrical distribution of the species richness per parasite group. The group with the highest species richness is the nematodes, and even though we cannot establish at this point the reason for this, we argue that it is due to some of the nematode genera occurring in Mexican freshwater fishes (e.g. *Rhabdochona*, with 12 species, see Aguilar-Aguilar *et al*. 2010) not conforming to monophyletic assemblages (Mejía-Madrid *et al*. 2007). This means that their diversification is not associated strictly with vicariance/dispersal events from the same ancestor. Instead, they seem to derive from different lineages from fishes whose affinities are found in both the Nearctic and Neotropical biogeographical regions.

Recent papers have discussed the appropriateness of taxonomic distinctness of parasite assemblages as an alternative measure of parasite diversity in comparative analyses (Luque *et al*. 2004; Luque and Poulin, 2008; Ponlet *et al*. 2011). However, we decided to use species richness since we were only looking for factors that influence species number in an assemblage and not the causes of a narrow or broad

Table 4. Coefficients obtained from generalized linear models performed on fish species values and results of multiple regressions of standardized independent contrasts (estimated through the origin) predicting species richness

(See Tables 1 and 2 for details of variables.)

	Total parasites				Ectoparasites				Endoparasites			
	Species		Contrasts		Species		Contrasts		Species		Contrasts	
Variable	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value
(Intercept)	0·83	7·25***			2·002e-02	0·20			2·84	1·93		
Size							2·47e-02	4·55***				
Regions	0·23	6·26***	0·92	4·12***	2·14e-01	4·56***	−1·14e-01	−0·77	−5·28–02	−0·77	0·29	1·42
Localities	0·05	6·43***	0·33	9·48***			5·41e-02	4·68***	7·50e-02	7·24***	0·28	9·02***
Trophic level									1·74e-01	2·64**		
MxL							−1·48e-01	−3·25**				
MnL							1·79e-01	2·80**	−8·03e-02	−2·26*		
ML							na	NA				
Length							1·59e-06	0·28				
Area							6·74e-06	3·38***				
Flow					2·74e-06	2·45*	9·58e-06	4·34***	5·47e-06	3·58***		
Basins							−2·68e-04	−0·04	5·96e-03	2·22*		
MAP	0·001	4·22***	0·002	2·76**			−5·10e-05	−0·14			0·002	2·65**
PDM	−0·01	−2·59**	−0·05	−2·36*			4·78e-04	0·06	−1·24e-01	−2·70**	−0·05	−2·47*
MTWM							9·23e-02	1·31	−2·08e-02	−0·51		
MTCM			0·01	0·07			−1·36e-02	−0·44			0·01	0·10
Flow:Basins							1·36e-06	9·61***				
Basins:MAP							−1·33e-04	−7·20***				
Size:MTCM							−2·10e-02	−6·91***				
Localities:MTCM			0·05	5·09***			3·14e-02	4·32***			0·04	4·73***
MnL:PDM									6·09e-03	2·40*		
Localities:PDM							−7·18e-03	−4·29***				
Regions:Localities	−0·01	−3·82***							3·32e-01	4·23***		
Regions:Basins							−2·37e-02	−7·09 ***				
Size:MTWM							−1·40e-02	−2·20*				
Localities:MTWM							−3·55e-02	−2·55*				
Area:PDM							−4·38e-07	−2·40*				
Length:PDM							9·36e-07	1·99*				
Localities:Flow							−6·25e-07	−2·70**				
Localities:MnL							−2·49e-02	−2·60*				
Regions:PDM			−0·05	−2·26*							−0·03	−1·60
Regions:MAP			−0·002	−2·88**							−0·002	−2·85**
Size:Localities:Area							−3·18e-08	−3·21**				
Size:Regions:Basins							2·11e-03	5·43***				
Basins:MAP:MTCM							−1·77e-05	−3·15**				
Area:Basins:MTWM							1·92e-07	4·57***				

Table 4. (*Cont.*)

	Total parasites				Ectoparasites				Endoparasites			
	Species		Contrasts		Species		Contrasts		Species		Contrasts	
Variable	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value
Length:Flow:MTWM							−1·25e-10	−4·002***				
Regions:Localities:Flow							2·26e-07	2·68**				
Regions:Localities:PDM			−0·006	−2·24*							−0·01	−2·24*
Regions:Localities:MTCM			0·02	2·79**							0·02	2·99**
Regions:Localities:MTCM									−1·04e-02	−4·31***		
p-value			<2·2e-16				<2·2e-16				<2·2e-16	
Adjusted R-squared			0·76				0·85				0·68	
Degrees of freedom			138				117				138	

Species, results of non-phylogenetic analyses; Contrasts, results of phylogenetic analyses; the sign indicates the direction of the effect; significance codes = 0 '***' 0·001 '**' 0·01 '*' 0·05 '.' 0·1 ' ' 1.

taxonomic range of parasite species in a host species, or we were not attempting to distinguish between the different origins of parasite species, an approach that necessarily requires detailed and robust phylogenetic hypotheses. Likewise, measurements of diversity that incorporate information on the relationships among parasite species would be necessary (i.e., taxonomic distinctness).

Patterns of species richness among hydrological regions show that southeastern areas of Mexico possess higher adult helminth species richness, whereas northern and central areas have lower richness. Previous studies have also pointed out that the geographical regions in which goodeids occur, i.e. central regions, are characterized by depauperate helminth communities in freshwater fishes (Espinosa-Huerta *et al.* 1996; Rojas *et al.* 1997, Pérez-Ponce de León *et al.* 2000; Sánchez-Nava *et al.* 2004), while the parasite communities of fishes occurring in southern regions are more diverse, i.e., Cichlidae (see Vidal-Martínez, 1995; Salgado-Maldonado and Kennedy, 1997). It has been argued that the basin's geological age, magnitude, and ichthyofaunal composition could explain those differences in helminth species richness among hydrological regions (Pérez-Ponce de León and Choudhury, 2005; Salgado-Maldonado *et al.* 2005). In addition, the biogeographical position of Mexico could be another explanation, since fish species occurring in the Nearctic or Neotropical region are not exposed to the same pool of parasite species. The size of the pool of available parasite species must differ from one geographical region to the next, and thus it can limit how many parasite species a host can acquire over time, regardless of the characteristics of this host species.

Several studies have searched for correlations between parasite diversity (in terms of species richness) and various fish host features such as body size, feeding habits, schooling behaviour and population density (for freshwater fishes: Poulin, 2001; Simková *et al.* 2001; Takemoto *et al.* 2005; Luque and Poulin, 2008; for marine fishes: Sasal *et al.* 1997; Morand *et al.* 2000; Luque *et al.* 2004; Luque and Poulin, 2004, 2008). However, there is no consensus regarding the role, if any, of these host traits in the evolutionary diversification of parasite faunas. Here, we found that adult helminth richness was not distributed randomly among freshwater fish species with respect to host traits and environmental and geographical factors. In addition to that, in the search for the factors that determine the parasite species richness, our study supports the need to take into account the transmission mode of the parasites, either direct or indirect (i.e., ectoparasites versus endoparasites), as has been shown in earlier studies (e.g., Luque and Poulin, 2004).

The results correspond in general with the patterns recognized previously by other authors at a comparable study scale. For instance, the distribution range,

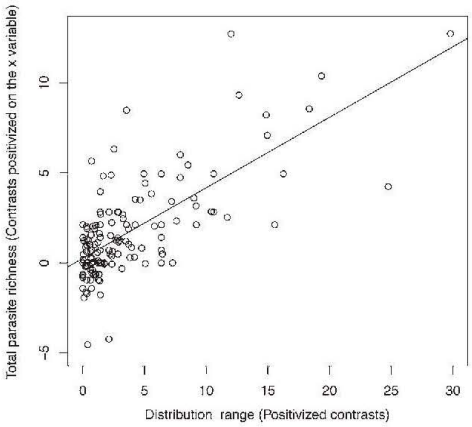

Fig. 2. Relationship between the total parasite species richness and the geographical range of the Mexican freshwater fish species (r = 0·62·85, p < 2·2e-16). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al.* (1992).

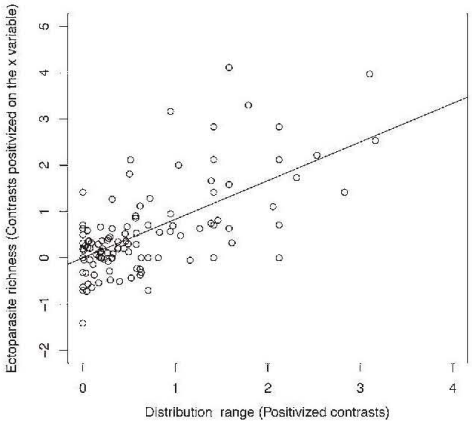

Fig. 3. Relationship between the ectoparasite species richness and the geographical range of the Mexican freshwater fish species (r = 0·5507, p < 2·2e-16). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al.* (1992).

host size, precipitation, temperature and latitude, appear to influence the number of parasite species exploiting a freshwater fish species. The host geographical range (the number of sites in which a host species occurs) was the main predictor of the species richness in our study. This characteristic correlated positively with parasite richness, i.e., fishes with broad geographical distributions have richer assemblages than those with limited distribution. This relationship suggests that new parasite species can be acquired in various geographical regions

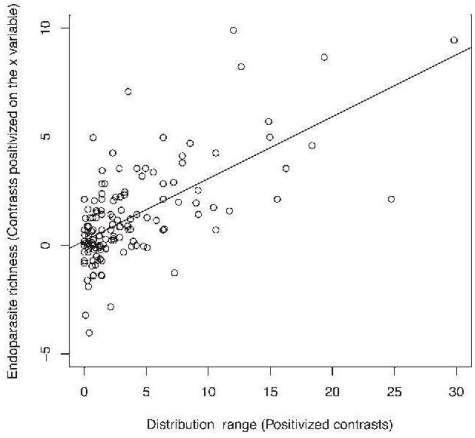

Fig. 4. Relationship between the endoparasite species richness and the geographical range of the Mexican freshwater fish species (r = 0·5497, p < 2·2e-16). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al.* (1992).

because fishes living across many localities feed on a wider array of prey species and therefore are exposed to colonization by more parasite species than fishes restricted to a narrow distribution. Under this scenario, fishes are also exposed to colonization by more ectoparasite species with the consequent increase in species richness.

A positive correlation between host body size and ectoparasite species richness was also found. This finding can be explained in the light of island biogeography theory (Kuris *et al.* 1980), where larger hosts offer a larger number of habitats for parasite colonization than smaller ones.

Another pattern detected in the present study was the correlation between the parasite species richness and latitude as well as precipitation and temperature of the distribution area of the fish species. This relation has been addressed in several earlier papers dealing with species richness and latitudinal gradients. Rohde (1992) and Rohde *et al.* (1995) observed that marine fish from tropical latitudes typically harbour richer ectoparasite communities than fish from temperate latitudes. Later, Poulin and Rohde (1997) suggested that the relationship between temperature and the marine-fish ectoparasite community richness was an indicator of the importance of temperature in the diversification of fish parasites in the tropics. Rohde and Heap (1998) confirmed that pattern, but they did not find a correlation between temperature and endoparasite species richness in marine fishes, suggesting that biological differences between ecto- and endoparasites may explain this difference. In accordance with Rohde (1992) the increase in parasite species diversity towards tropical areas is the result of higher diversification rates or

effective evolutionary time, which are correlated with temperature. In the case of freshwater fishes a negative relationship between parasite species richness and temperature has been observed (Choudhury and Dick, 2000; Poulin, 2001). However, in a more recent study Luque and Poulin (2008) found a positive correlation between the parasite taxonomic distinctness of freshwater fishes from the Neotropical Region and temperature for all parasites and for ectoparasites and endoparasites treated separately. Apparently, in marine and freshwater environments, temperature is a major force driving not only the increase in the number of parasite species but also the increase of their taxonomic complexity over evolutionary time, mediated by greater rates of speciation and host colonization (Poulin and Morand, 2004).

Trophic level (host feeding habits, host diet or trophic category) influenced endoparasite species richness, but only when the analyses were conducted with fish species values, i.e., fish species at higher trophic levels may not only acquire more parasites through their diet, but also they may be exposed to a broader range of different parasite taxa. This pattern was only evident when endoparasite assemblages were analysed separately, because helminth endoparasites are usually acquired by ingestion due to their indirect life cycle. For instance, predatory fish (fishes with higher trophic levels) should be exposed to more infective helminth larvae in their diet than planktivores. Over evolutionary time, this should translate in higher parasite colonization rates in predatory fish than in planktivorous fish, pushing up the equilibrium of parasite species richness.

Another host trait that was evaluated in this paper was the position of the host in the water column and its relation with parasite species richness. In particular, no correlation was found between these two variables even though previous studies have shown that benthic fish may harbour more directly transmitted parasite species than pelagic fish. The reason for that pattern has not been identified for freshwater fish parasites, although it has been argued that the benthic boundary layer is a focal point for parasite exchange among faunas inhabiting different vertical zones in marine habitats (Marcogliese, 2002).

Finally, on a larger scale, several other important factors can influence the parasite species distribution and the diversification of parasite assemblages in Mexican fish (e.g. high levels of endemism in certain river basins (Domínguez-Domínguez *et al.* 2006; Huidobro *et al.* 2006) and a significant number of exotic species introduced in the region). Therefore, the patterns uncovered in this study support the contention that parasite diversity, in this case parasite species richness, is largely affected by both host ecology and biogeography.

Although our approach uses the best available data for the helminth parasites of freshwater fishes, our attempts to identify the factors that determine parasite species richness are preliminary and provide but a glimpse of the patterns and processes that determine the species distribution of the helminth fauna of freshwater fish. Further sampling needs to be conducted in certain host families and particular river basins along the country, even though, as stated by Pérez-Ponce de León and Choudhury (2010), the inventory of the helminth parasite fauna in freshwater fishes in Mexico may be nearing completion (with the exception of the monogeneans).

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DISCUSION GENERAL

Una manera de acercarnos al estudio de los patrones de distribución geográfica de la biota es a través de una perspectiva macroecológica. En el presente trabajo se examinaron patrones macroecológicos de los peces dulceacuícolas de México y sus helmintos adultos para contribuir al conocimiento en este campo de investigación, ya que la mayoría de los estudios de estas faunas se han centrado en otras áreas de la biología. Esta exploración permitió documentar los patrones de variación espacial de la riqueza de especies de ambos grupos taxonómicos y en el caso de los peces también se describieron los patrones del tamaño corporal y del tamaño de sus áreas de distribución.

La variación espacial de la riqueza de especies ha sido documentada para diferentes grupos taxonómicos de distintas formas de vida y ambientes y en varias escalas geográficas (Storch y Gaston, 2004; Poulin, 2004). Algunas de las hipótesis a las que frecuentemente se recurre para explicar el patrón a escalas grandes son: la relación especies-área, la relación especies-energía y la hipótesis histórica (Storch y Gaston, 2004; Poulin, 2004; Oberdorff *et al*., 1997). La hipótesis especies-área afirma que el número de especies aumenta a medida que se incrementa el área geográfica, la hipótesis especies-energía predice una correlación positiva entre la riqueza de especies y la energía disponible en el sistema, y la hipótesis histórica explica los gradientes de diversidad, al menos a escala global, por patrones de recolonización y maduración de ecosistemas después de la última glaciación.

Los resultados de este trabajo de tesis sugieren que no existe un único factor que determine la variación espacial del número de especies en ambientes dulceacuícolas. Los determinantes de la riqueza de especies ícticas fueron primero las variables relacionadas con procesos históricos y después aquellas concernientes al tamaño del área. Los factores históricos reconocidos en regiones de latitudes altas del Hemisferio Norte (por ejemplo, Europa y el norte de Norte América) están relacionados con la recolonización y maduración de ecosistemas después de la última glaciación (por ejemplo, Oberdorff *et al*., 1997). Sin embargo, en México los determinantes históricos tienen que ver con la evolución geomorfológica de las redes hidrográficas, lo cual ha determinado eventos de especiación vicariante que promueven la riqueza de las ictiofaunas en distintas regiones hidrológicas (para ejemplos ver Domínguez-Domínguez *et al*., 2006; Ornelas-García *et al*., 2008; Pérez-Rodríguez *et al*., 2009).

La relación especies-área ha sido reportada como la explicación principal al patrón de variación geográfica de la riqueza de especies de varios ensamblajes de peces dulceacuícolas (ver Oberdorff *et al*., 2011 y literatura citada ahí). Sin embargo, los análisis de los peces dulceacuícolas mexicanos señalan que las variables relacionadas con el tamaño del hábitat sólo son determinantes secundarios del número de especies y confirman que esta relación se debe a la diversidad de hábitats, lo que sugiere que a medida que el área se incrementa, aumenta el número de hábitats y la cantidad de recursos alimenticios, proveyendo de este modo de más nichos y conteniendo más especies. En contraste, los datos no corroboran la explicación a la relación especies-área que sugiere como determinantes del número de especies a los procesos de especiación y extinción que ocurren a escalas de tiempo evolutivo, señalando que las áreas grandes, favorables y estables podrían sustentar poblaciones con mayor abundancia total, lo cual incrementaría el número de individuos disponibles para que ocurra especiación, resultando en un incremento local de la riqueza de especies.

Los patrones de distribución de la riqueza de especies de peces también han sido explicados por la relación especies-energía (ver Heino, 2011 y referencias citadas ahí). La hipótesis propone que la energía restringe la riqueza de especies a través de cascadas tróficas o requerimientos fisiológicos de los organismos (Storch y Gaston, 2004). No obstante, los estudios de peces dulceacuícolas únicamente han evaluado los límites relacionados con los insumos de energía disponibles en el área geográfica tales como la temperatura, precipitación, etc. (por ejemplo, Oberdorff *et al*., 1997; Griffiths, 2010). A escalas amplias, las variables climáticas, tales como la temperatura, usualmente representan los mejores predictores de riqueza de especies ícticas en los trópicos y subtrópicos, mientras que las variables como la evapotranspiración, precipitación y productividad dominan en zonas templadas (Oberdorff *et al*., 2011). Sin embargo, los resultados de esta investigación no sugieren ningún factor energético como determinante del número de especies, cuando factores históricos son considerados. Por lo mismo, más estudios que incluyan, entre otros, la mayoría de los factores de tipo histórico y energético son necesarios en diferentes regiones del mundo, para confirmar la importancia de uno, otro o ambos en la conformación de los patrones de distribución de estas especies.

Por otra parte, el reconocimiento de los factores que determinan los patrones de variación de la riqueza de especies de parásitos representa un reto aún mayor que para organismos de vida libre, pues algunos de los posibles determinantes de riqueza parasitaria podrían ser la

consecuencia y no la causa de una fauna de parásitos rica (por ejemplo, en el tiempo evolutivo, un linaje de huéspedes que alberga numerosas especies de parásitos está bajo selección fuerte para desarrollar varias adaptaciones anti-parásitos). A pesar de está limitante, en los últimos años se han publicado algunos trabajos documentando la variación de la riqueza de especies parasitas entre las especies de huéspedes (ver la revisión de Poulin, 2004). Los factores señalados como determinantes de la riqueza de especies frecuentemente han estado relacionados con la hipótesis especies-área (tamaño del área de distribución y tamaño corporal) (Luque y Poulin, 2008). Los resultados de este trabajo confirman esos hallazgos, pero el área de distribución de los huéspedes fue la única característica relacionada con el tamaño del hábitat que determinó las riquezas de los helmintos en los peces distribuidos dentro del territorio mexicano. Además nosotros sugerimos que la localización geográfica de las áreas de distribución de los huéspedes también contribuye a la adquisición de nuevas especies, es decir, los huéspedes con áreas de distribución amplias y ubicadas en la zona de transición biogeográfica tienen una mayor oportunidad de adquirir nuevas especies de parásitos.

La hipótesis especies-energía también fue apoyada por los datos de los helmintos, pues los análisis confirman parcialmente que la latitud/temperatura son determinantes de la riqueza de especies de ectoparásitos. Poulin (2004) sugirió que la riqueza de este tipo de parásitos es mayor en los trópicos que en las áreas templadas, debido a que las temperaturas elevadas se asocian con tiempos de generación más cortos e índices de mutación más altos y en consecuencia índices de especiación y evolutivos más altos.

Otros patrones macroecológicos fueron explorados para los peces dulceacuícolas (patrones del tamaño corporal y del tamaño de sus áreas de distribución), pero en ningún caso se buscaron las causas que los determinan. Básicamente, se reconoce que como en otros ensamblajes de peces dulceacuícolas (por ejemplo, Griffiths, 2010; 2011) se cumplen tanto la regla de Rapoport como la de Bergmann (incremento progresivo del tamaño de las áreas de distribución geográfica y el tamaño corporal a medida que la latitud se incrementa, respectivamente). De acuerdo con Storch y Gaston, 2004, los procesos posibles que subyacen a estos patrones son: 1) una mayor capacidad de dispersión de las especies de zonas templadas, aunada a una mayor tasa de extinción en las especies de talla mayor en zonas tropicales, y 2) la existencia de nichos ecogeográficos más estrechos en las zonas tropicales.

Los resultados de está investigación nos permiten proponer que los patrones descritos para los peces dulceacuícolas son lo suficientemente sólidos y estables como para modificarse, aun cuando se trabaje con un mayor conjunto de datos. Sin embargo, en el caso de los helmintos el incremento de los muestreos probablemente nos permita obtener un patrón más robusto de la variación espacial de la riqueza de especies, pues sólo se ha estudiado una parte del componente ictiológico (aproximadamente el 50%) y algunos sistemas hidrológicos han sido explorados parcialmente (por ejemplo, Sonora Sur, algunas de la Península de Baja California y varias ubicadas en las costas del occidente), en tanto que otros no han sido muestreados aún (por ejemplo, Sinaloa, Sonora Norte). No obstante, lo anterior no quiere decir que el inventario de los helmintos se incrementará proporcionalmente a los muestreos, pues se ha reconocido que cada familia de huéspedes posee un conjunto particular de helmintos.

CONCLUSIONES GENERALES

♦ El grupo de los peces dulceacuícolas nativos de México incluye más de 400 especies, de las cuales aproximadamente 60% son endémicas del territorio nacional. De ellas, únicamente 149 especies han sido registradas como huéspedes de 160 especies de helmintos adultos.

♦ El ensamblaje de los peces y el de los helmintos incluyen elementos de los componentes biogeográficos neártico y neotropical, así como elementos de la zona de transición.

♦ La mayoría de las especies de peces son pequeñas y tienen áreas de distribución reducidas.

♦ El tamaño de las áreas de distribución geográfica de las especies de peces presenta un claro efecto Rapoport, es decir, el tamaño de las áreas incrementa progresivamente conforme se alcanzan latitudes más elevadas.

♦ La regla de Bergmann también se cumple para los peces dulceacuícolas de México, lo que significa que el tamaño corporal de las especies tiende a ser mayor si la latitud se incrementa.

♦ La riqueza de especies de peces varía a través las regiones hidrológicas, debido a factores históricos y al tamaño del hábitat (los hábitats más grandes y las regiones ubicadas en la zona de transición biogeográfica y con más aislamientos geográficos de sus cuencas albergan los ensamblajes de peces más ricos).

♦ El número de especies de helmintos varía entre las especies de peces, lo cual depende esencialmente del tamaño del área de distribución del huésped (los peces más ampliamente distribuidos son parasitados por un mayor número de especies de helmintos).

♦ Los patrones descritos para los peces dulceacuícolas son lo suficientemente robustos para mantenerse aun cuando se incremente la muestra analizada. Sin embargo, los datos de los helmintos indican que sólo se ha estudiado una parte del ensamblaje ictiológico y algunos sistemas hidrológicos, por lo que, un mejor conjunto de datos permitirá describir patrones de variación espacial de la riqueza de especies más sólidos.

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