



Distributional patterns of freshwater taxa (fishes, crustaceans and plants) from the Mexican Transition Zone

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ABSTRACT

Aim To test whether distributional patterns of Neotropical freshwater taxa fit the generalized tracks already postulated for terrestrial groups occurring in the Mexican Transition Zone.

Location The study units comprised 17 hydrological basins located along the Pacific coast of the Americas from Mexico to Panama, and in the Gulf of Mexico from the Papaloapan to the Grijalva–Usumacinta basin.

Methods Distributional data for 22 fish species, 34 crab species of the tribe Pseudothelphusini, and 22 strictly freshwater species of angiosperms were analysed. Parsimony analysis of endemism is based on presence/absence data of these taxa and uses the computer programs Winclada and NONA.

Results Three generalized tracks were obtained: (1) Mexican North Pacific, (2) Mexican Central Pacific, and (3) Southern Mexico–Guatemala. A node resulted at the intersection of the first two tracks, coinciding with the Neovolcanic Axis in central Mexico.

Main conclusions Freshwater generalized tracks with an altitudinal distribution below 1000 m, mainly including fishes and angiosperms, are close to the Tropical Mesoamerican generalized track. Generalized tracks above 1000 m, including freshwater crabs, have a stronger affinity with the Mountain Mesoamerican track. The Isthmus of Tehuantepec represents a node for the Neotropical freshwater and terrestrial biota. These results seem to indicate that common geobiotic processes have induced these patterns.

Keywords

Angiosperms, Crustacea, freshwater fishes, historical biogeography, hydrological basins, Neotropics, PAE, panbiogeography, tracks.

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INTRODUCTION

The Mexican Transition Zone (MTZ) was defined by Halffter (1972, 1974, 1976, 1978, 1987, 2003) as a complex area in which Neotropical and Nearctic biotic components overlap; it includes south-western USA, Mexico, and a large part of Central America. Halffter (1987) analysed distributional patterns of species of montane Scarabaeidae (Coleoptera) in the MTZ, categorizing them as Mountain Mesoamerican, Palaeoamerican, or Nearctic distributional patterns. Morrone & Márquez (2001) undertook a panbiogeographical analysis based on beetle (Coleoptera) taxa from the MTZ, and found two generalized tracks: a northern

generalized track, comprising basically mountain areas, which corresponds to the Mountain Mesoamerican distributional pattern; and a southern generalized track, basically in lowland areas, which corresponds to a Tropical Mesoamerican distributional pattern. Further analyses of the MTZ have involved terrestrial taxa (Liebherr, 1991, 1994; Ortega & Arita, 1998; Marshall & Liebherr, 2000; Contreras-Medina & Eliosa-León, 2001; Morrone & Márquez, 2001, 2003; Ochoa *et al.*, 2003; Escalante *et al.*, 2004; Morrone & Gutiérrez, 2005), but studies dealing with freshwater taxa are scarce (Brooks & Mayden, 1992; Mateos *et al.*, 2002; Aguilar-Aguilar *et al.*, 2003; Mateos, 2005; Pérez-Ponce de León & Choudhury, 2005).

Mexican freshwater environments have been constantly modified by the dynamic history of the MTZ, essentially as a result of intense tectonic and volcanic activities. These changes are reflected in the fragmentation of the hydrological basins, namely the closed (endorheic) basin in northern and central Mexico (Miller & Smith, 1986), and the basins associated with the coastal plains of the Atlantic and Pacific slopes, delimited by the Sierra Madre Occidental, Sierra Madre Oriental, and Sierra Madre del Sur. The evolution of freshwater organisms such as fishes, crustaceans and angiosperms along the MTZ may have been influenced by intense vicariance events associated with its geological history. The MTZ represents the overlap of Nearctic and Neotropical biotic components. This overlap is particularly evident in southern and central Mexico, where the Neovolcanic Axis or Transmexican Volcanic Belt is one of the most notable orographic features within this zone, characterized by extensive and complex geological processes (Savage, 1966; Duellman, 1970; Halffter, 1976, 2003; Demant, 1978; Rzedowski, 1978; Miller & Smith, 1986).

Most previous studies focused mainly on taxa distributed at altitudes above 1000 m across the mountainous chains of the Sierra Madre Occidental, Sierra Madre Oriental and Sierra Madre del Sur. It would be interesting to determine if the observed patterns are shared by taxa distributed below 1000 m, which apparently have different biogeographical affinities (Halffter, 1987; Morrone & Márquez, 2003).

Our goal is to identify generalized tracks for three freshwater groups from the MTZ and to determine whether they are congruent with the generalized tracks identified by previous authors for terrestrial taxa.

MATERIALS AND METHODS

Study area

We analysed 17 hydrological basins (Fig. 1) from southern Arizona in the USA to southern Central America. Eleven of them are located on to the Mexican Pacific slope, three are along the

south-western Gulf of Mexico slope, two are on the Pacific side of Central America, and one is an inner basin in central Mexico. All units were delimited according to hydrological maps from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Tamayo (1962), and INEGI-IG (2003). Miller (1986) defined 27 hydrological basins for Mexico, based on the presence of endemic fish; some of them correspond to the distribution of the taxa analysed herein. Hydrological basins were considered as units for the analysis, they are defined based on the common physiographical characteristics found in the areas contained within each basin and on the possibility of defining their limits with the aid of topographical and geological attributes (Álvarez & Cassián, 1993).

Fish data set

Distributional data for 22 species of *Poeciliopsis* were analysed: *P. baenschii*, *P. balsas*, *P. catemaco*, *P. elongata*, *P. fasciata*, *P. gracilis*, *P. hnilickai*, *P. latidens*, *P. lucida*, *P. lutzi*, *P. infans*, *P. monacha*, *P. maldonadoi*, *P. occidentalis*, *P. paucimaculata*, *P. presidionis*, *P. prolifica*, *P. retropinna*, *P. scarlli*, *P. turneri*, *P. turubarensis*, and *P. viriosa*. The geographical distribution of each species was determined from the information contained in the NEODAT (Inter-Institutional Database of Fish Biodiversity in the Neotropics) and BIOTICA data bases, which correspond to the following ichthyological collections: Colección Nacional de Peces, Instituto de Biología, UNAM (CNPE); Escuela Nacional de Ciencias Biológicas-Peces, IPN (ENCB-P); Universidad Autónoma de Nuevo León (UANL); Departamento de Investigaciones Científicas y Tecnológicas de la Universidad de Sonora (DICTUS); Colección Ictiológica, Universidad Michoacana San Nicolás de Hidalgo, Morelia (CIUMSNH); National Museum of Natural History, Washington, DC (USNM); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Universidad de Costa Rica (UCR); and Field

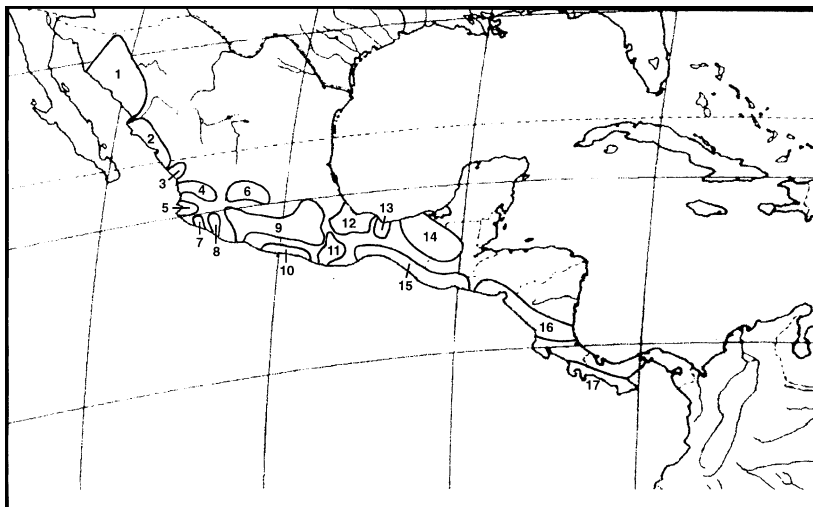


Figure 1 Hydrological basins with the presence of at least two of the groups of aquatic organisms considered in this study. 1, Sonora-Mayo; 2, Coastal Sinaloa; 3, Acaponeta-San Pedro; 4, Santiago; 5, Ameca; 6, Lerma; 7, Nicolás-Cihuatlán; 8, Armería-Coahuayana; 9, Balsas; 10, Papagayo-Ometepec; 11, Verde; 12, Papaloapan-Jalcomulco; 13, Coatzacoalcos; 14, Grijalva-Usumacinta; 15, Tehuatepec-Guatemala; 16, Lempa-San Juan; 17, Nicoya-Tonosi.

Museum of Natural History, Chicago (FMNH). Additional data were taken from Álvarez & Aguilar (1957), Miller (1960, 1966, 1975, 1986), Rosen & Bailey (1963), Álvarez del Villar (1970), Meyer & Vogel (1981), Meyer *et al.* (1985, 1986), Lozano & Contreras (1987), Lyons & Navarro (1990), Page & Burr (1991), Espinosa *et al.* (1993), and Bussing (1998).

Crustacean data set

Distributional data for 34 species of crabs of the tribe Pseudothelphusini were analysed: *Disparithelphusa pecki*, *Pseudothelphusa americana*, *P. belliana*, *P. digueti*, *P. dilatata*, *P. doenitzi*, *P. dugesi*, *P. galloi*, *P. granatensis*, *P. guerreroensis*, *P. hoffmannae*, *P. jouyi*, *P. leiophrys*, *P. lophophallus*, *P. mexicana*, *P. morelosis*, *P. nayaritae*, *P. nelsoni*, *P. parabelliana*, *P. peyotensis*, *P. rechingeri*, *P. seiferti*, *P. sonorensis*, *P. sulcifrons*, *P. terrestris*, *Smalleyus tricristatus*, *Tehuana complanata*, *T. chontalpaensis*, *T. diabolis*, *T. jacatepecensis*, *T. lamellifrons*, *T. lamothei*, *T. poglayenorum*, and *T. veracruzana*. The geographical information for these species was obtained from specimens deposited in the Colección Nacional de Crustáceos (CNCR) of the Instituto de Biología, UNAM, and the National Museum of Natural History, Washington, DC (USNM).

Aquatic angiosperm data set

Twenty-two strictly freshwater species of angiosperms were analysed: *Eichornia heterosperma*, *Heteranthera oblongifolia*, *H. spicata*, *Hydrocheys parviflora*, *Limnocharis flava*, *L. laforestii*, *Marathrum rubrum*, *M. schiedeanum*, *M. tenue*, *Nelumbo lutea*, *Nymphaea amazonum*, *N. ampla*, *N. conardii*, *N. elegans*, *N. jamesoniana*, *N. mexicana*, *N. odorata*, *N. prolifera*, *Oserya coulteriana*, *O. longifolia*, *Podostemum ricciiiforme*, and *Vanroyenella plumosa*. Distributional data for each species were obtained from Lot *et al.* (1999).

Data analysis

Morrone (2001a) suggested that the panbiogeographical method (Craw *et al.*, 1999) could be applied as a first step of a biogeographical analysis to identify common distributional patterns or generalized tracks, which could then be tested through a cladistic biogeographical analysis (Humphries & Parenti, 1999). The panbiogeographical method uses the distribution of each species represented on a map to obtain individual tracks. After many species have been added to the data set, their overlap provides generalized tracks, which are taken to indicate the pre-existence of ancestral biotic components that have been fragmented by tectonic or climatic changes (Morrone & Crisci, 1995; Craw *et al.*, 1999). Parsimony analysis of endemism or PAE (Rosen, 1988; Morrone, 1994; Morrone & Crisci, 1995) is a quantitative implementation of panbiogeography that classifies areas that share at least two species or supraspecific taxa in order to elucidate possible biotic relationships. An absence/presence matrix representing each species for every hydrological basin was constructed (see

Supplementary Material). PAE was carried out using the computer programs Winclada version 0.9.99 (Nixon, 1999) and NONA version 2.0 (Goloboff, 1993). Cladograms were rooted with a hypothetical basin coded with zeros for all species. Luna Vega *et al.* (2000), García-Barros *et al.* (2002), and García-Barros (2003) proposed PAE-PCE (PAE with progressive character elimination), which consists of applying successive parsimony analyses, eliminating in each run the synapomorphic species that define the area clades. This procedure results in alternative groups of areas to the most parsimonious arrangement. From the consensus cladograms obtained in each run, area clades supported by at least two taxa were mapped as generalized tracks. Nodes indicating composite areas were identified where different generalized tracks overlapped (Morrone & Crisci, 1995; Grehan, 2001).

RESULTS

Based on the 96 taxa analysed, 76 individual tracks were obtained with at least two localities recorded for each one (Figs 2–5); the remaining 20 species are known from a single locality.

Parsimony analysis of endemism produced 12 cladograms. The consensus cladogram had 140 steps, a consistency index of 0.58, and a retention index of 0.55 (Fig. 6a); it depicts three groups of basins, which can be used to identify three generalized tracks. The first track covers the area between the Sonora-Mayo basins, the Sinaloa coast, the Acaponeta-San Pedro basins, and the Santiago basin; it is defined by three species, namely *Poeciliopsis latidens*, *P. presidionis* and *P. prolifica*. The second track groups the Nicolás-Cihuatlán and Armería-Coahuayana basins, and is defined by *Poeciliopsis baenschii*, *P. turneri* and *Pseudothelphusa seiferti*. The third track covers the Grijalva-Usumacinta and Tehuantepec-Guatemala basins, and is defined by *Poeciliopsis hnulickai* and the genus *Tehuana*.

The second analysis applied (PAE-PCE) produced 33 cladograms. The consensus cladogram (Fig. 6b), with a length of 149 steps, consistency index of 0.59, and retention index of 0.54, allowed us to identify three generalized tracks (Fig. 7). The first one, named Mexican North Pacific (I), extends from northern Sonora in the Sonora river basin to the Ameca basin, Jalisco. This track is supported by the individual tracks of six species: *Poeciliopsis latidens*, *P. lucida*, *P. monacha*, *P. presidionis*, *P. prolifica* and *P. viriosa*. The second generalized track, named Mexican Central Pacific (II), ranges from the San Nicolás river basin, Jalisco, to the Coahuayana river basin, on the border between Colima and Michoacán; it consists of two species, namely *Poeciliopsis baenschii* and *P. turneri*. The overlap of the first two generalized tracks results in a node located on the western border of the Neovolcanic Axis, on the Pacific slope. The third generalized track, named South Mexico–Guatemala (III), joins the Papaloapan-Jalcomulco and Grijalva-Usumacinta river basins with the Tehuantepec river, and Oaxaca with northeastern Guatemala. In this generalized track we found three endemic taxa: the fish *Poeciliopsis hnulickai*, crabs of the genus *Tehuana*, and the plant *Nymphaea conardii*.

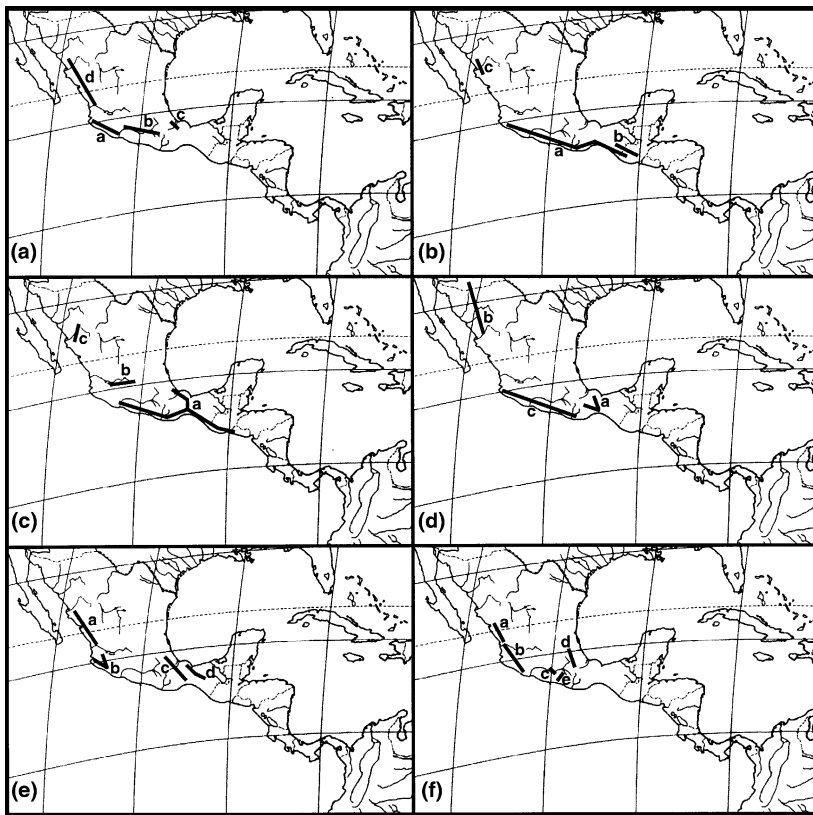


Figure 2 Individual tracks. (a) a, *Poeciliopsis baenschii*; b, *P. balsas*; c, *P. catemaco*; and d, *P. latidens*. (b) a, *P. fasciata*; b, *P. hnlickai*; and c, *P. lucida*. (c) a, *P. gracilis*; b, *P. infans*; and c, *P. monacha*. (d) a, *P. lutzi*; b, *P. occidentalis*; and c, *P. scarlli*. (e) a, *P. presidionis* and *P. prolifica*; b, *P. turneri*; c, *Tehuana jacatepecensis–complanata–lamellifrons* species group; and d, *T. chontalpaensis–poglaeyerorum–veracruzana* species group; (f) a, *Poeciliopsis viriosa*; b, *Pseudothelphusa peyotensis–leiophrys–terrestris* species group; c, *P. granatensis–mexicana* species group; d, *P. americana–doenitzi* species group; and e, *P. belliana–hoffmanae* species group.

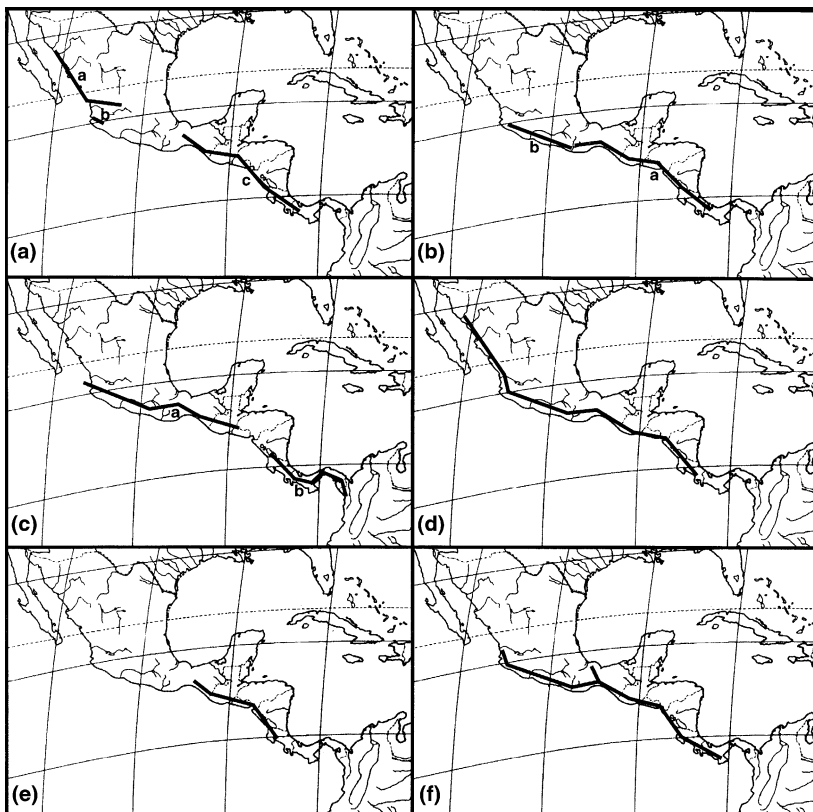


Figure 3 Individual tracks. (a) a, *Pseudothelphusa jouyi–sonorensis–nayaritae–lophophallus–rechingeri* species group; b, *P. dilatata–seiferti* species group; and c, *Eichornia heterosperma*. (b) a, *Heteranthera oblongifolia*; and b, *Marathrum rubrum*. (c) a, *Limnocharis laforestii*; and b, *Heteranthera spicata*. (d) *Limnocharis flava*. (e) *Hydrocleys parviflora*. (f) *Marathrum schiedeanum*.

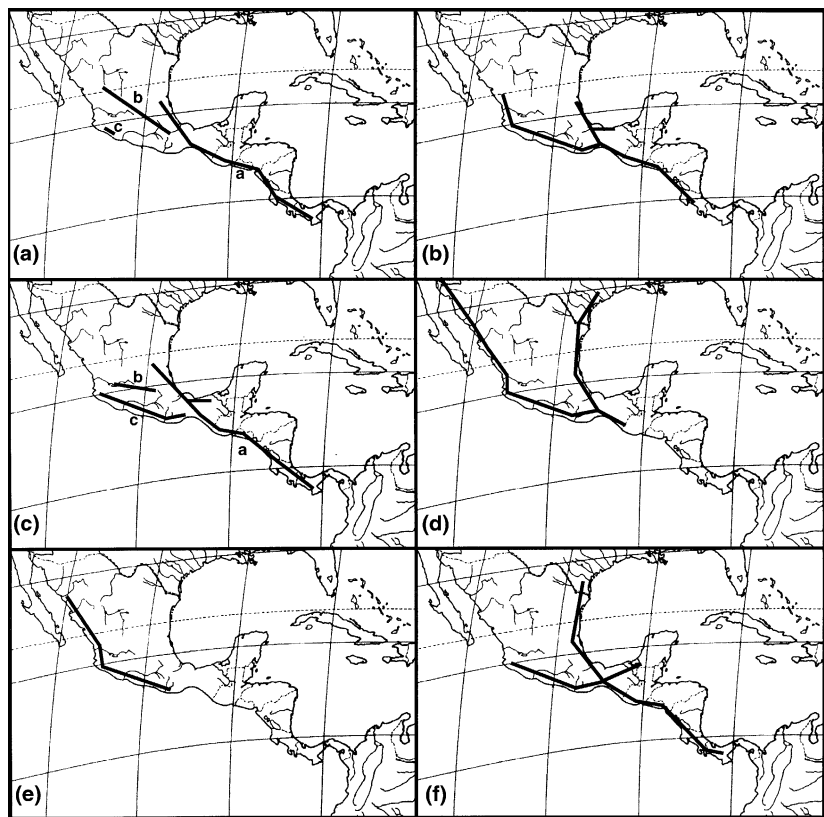


Figure 4 Individual tracks. (a) a, *Marathrum tenue*; b, *Nymphaea gracilis*; and c, *Oserya longifolia*. (b) *Nelumbo lutea*. (c) a, *Nymphaea amazonum*; b, *N. mexicana*; and c, *Vanroyenella plumose*. (d) *Nymphaea elegans*. (e) *Oserya coulteriana*. (f) *Nymphaea jamesoniana*.

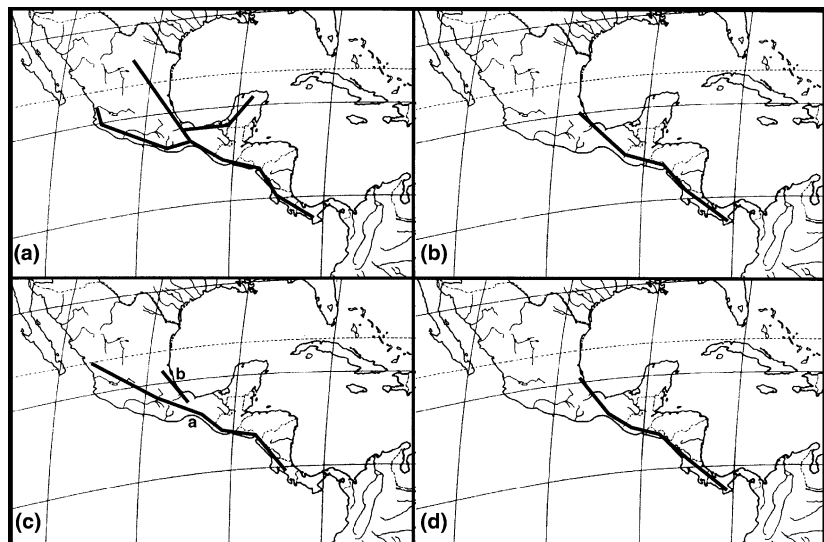


Figure 5 Individual tracks. (a) *Nymphaea ampla*. (b) *N. conardii*. (c) a, *N. odorata*; b, *Podostemum ricciiforme*. (d) *Nymphaea prolifera*.

Both PAE and PAE-PCE produced very similar results. This may indicate the existence of clear distributional patterns.

DISCUSSION

Freshwater environments in Mexico have received great attention because of their importance for agriculture and energy generation, and in particular for their role as reservoirs of biological diversity (Arriaga *et al.*, 2000). Around 320 hydrological basins have been recognized in Mexico (García,

1982; SEDESOL, 1993); 19 drain to the Pacific Ocean, 12 to the Gulf of Mexico and the Caribbean, and six are closed basins. Along both slopes, the drainage systems originate in the higher parts of mountain ranges and smaller sierras, and are divided by a series of topographic features that isolate freshwater communities, including aquatic plants, crustaceans and fish. Both freshwater crustaceans and fish are characterized by a reduced dispersal capability, favouring the emergence of similar distributional patterns resulting from the geological evolution of the basins.

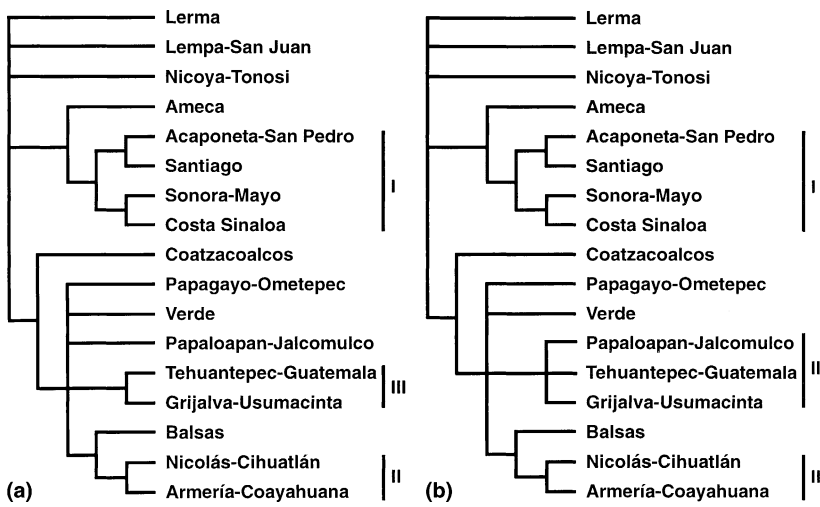


Figure 6 Strict consensus cladograms: (a) PAE, with 140 steps, CI = 0.58, and RI = 0.55; (b) PAE-PCE, with 149 steps, CI = 0.59, and RI = 0.54. Roman numerals indicate the main clades, which contain at least two species or supraspecific taxa.

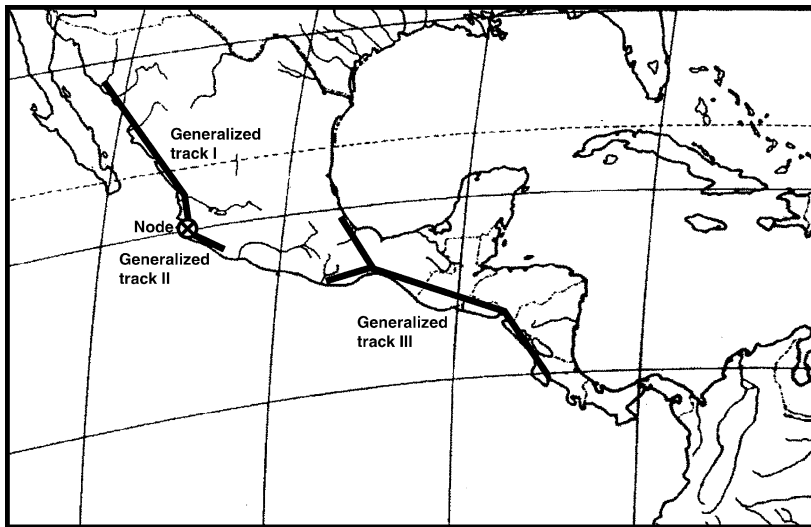


Figure 7 The three generalized tracks obtained in this study: I, Mexican North Pacific, extending from northern Sonora in the Sonora river basin to the Ameca basin, Jalisco; II, Mexican Central Pacific, from the San Nicolás river basin, Jalisco, to the Coahuayana river basin, along the border between Colima and Michoacán; III, South Mexico–Guatemala, joining the Papaloapan–Jalcomulco and Grijalva–Usumacinta river basins with the Tehuantepec river, and Oaxaca with northeastern Guatemala.

Three generalized tracks were recognized in this study, all restricted to the Pacific slope: Mexican North Pacific (I), Mexican Central Pacific (II), and South Mexico–Guatemala (III). They are similar to other tracks that have been identified previously for Mexico: the Pacific Coast track of Miller & Smith (1986), the Tropical Mesoamerican track of Morrone & Márquez (2001, 2003), and the South American track of Contreras-Medina & Eliosa-León (2001).

Regarding generalized track I, six species of *Poeciliopsis* represent an endemic group for the Mexican north Pacific, which is limited to the south by the Neovolcanic Axis. The distribution of these species is particularly congruent with the Pacific Coast track of Miller & Smith (1986), because of the affinity of these species with low-altitude habitats located along the western slope of the Sierra Madre Occidental. This area forms a geologic continuum inside the Northeast Coastal Plain morphotectonic province (Ferrusquía-Villafranca, 1993), precisely where the Sierra Madre Occidental approaches and reduces the coastal plain to form its narrowest section. Five species of crustaceans were registered as autapomorphies of the

Sonora-Mayo and Santiago basins on the slope of the Sierra Madre Occidental: *Pseudothelphusa lophophallus*, *P. nayaritae*, *P. peyotensis*, *P. rechingeri* and *P. sonorensis*. The last two species define the northern limit of the family Pseudothelphusidae. The same is true of *Poeciliopsis occidentalis* for the genus *Poeciliopsis*. The distributional patterns of several of the aquatic angiosperms analysed herein are very similar to those of the species of *Poeciliopsis*, mainly on the Mexican Pacific slope and the Sierra Madre del Sur. Nevertheless, angiosperms do not show a distributional pattern that can be identified as a generalized track, because their distributional ranges include other areas as well.

Generalized track II, the Mexican Central Pacific track, encompasses a restricted area located south of the Neovolcanic Axis. It is delimited to the north by the San Nicolás basin, in the state of Jalisco, and to the south by the Coahuayana river, between the states of Colima and Michoacán. This track is defined by two endemic fishes: *Poeciliopsis baenschi* and *P. turneri*. Similarly to the case for track I, there were neither crustaceans nor angiosperms supporting this generalized track.

Inside the hydrological basins involved, however, there is a group of freshwater crabs with particular distributional patterns: *Pseudothelphusa seiferti*, which has a widespread distribution along the Pacific slope of the Cacoma, Manantlán and Perote sierras, occurring in tributaries of large rivers such as the Marabasco, Armería and Tuxpan; and a group of species, which are very similar morphologically, including *Pseudothelphusa* aff. *peyotensis*, *P. terrestris* and *P. leiophrys*, which occur along a north–south track from western Nayarit to the west end of the Lerma basin and the Neovolcanic Axis. These species seem to be distributed along the Colima graben, and in the states of Jalisco and Nayarit, along the Tepic–Zacoalco graben (Mateos *et al.*, 2002).

As a result of the overlap of generalized tracks I and II, we located a node at the western end of the Neovolcanic Axis (Fig. 7). This node is located within the MTZ, where Nearctic and Neotropical biotic elements are in contact (Miller, 1966; Bussing, 1976, 1985; Brooks & Mayden, 1992). The complexity of the MTZ arises not only because of the mixing of different biotic elements, but also because it represents a centre of diversification for several groups (Franco-Rosselli & Berg, 1997; Morrone & Gutiérrez, 2005). *Poeciliopsis baenschii*, *P. turneri* and *Pseudothelphusa seiferti*, endemic species of the Armería–Coahuayana basins, are distributed in the western portion of the proposed node. All these elements combined support Heads' (2004) notion of how a node is defined.

The taxa analysed in this study have been greatly influenced by the emergence of the Neovolcanic Axis in central Mexico, an event that resulted in the isolation of various groups of species in the Lerma basin to the north, and in the Balsas basin to the south (Halffter, 1987; Marshall & Liebherr, 2000; Mateos *et al.*, 2002; Mateos, 2005). North of the Neovolcanic Axis, the genus *Poeciliopsis* presents seven species corresponding to track I, namely *P. latidens*, *P. lucida*, *P. monacha*, *P. occidentalis*, *P. presidionis*, *P. prolifica* and *P. viriosa*, whereas *Pseudothelphusa* presents four species, namely *P. lophophallus*, *P. nayaritae*, *P. rechingeri* and *P. sonorensis*. It is notable that the localities where these species have been collected are all at altitudes ranging from 20 to 600 m. A second group is located between tracks I and II, represented by the fish *Poeciliopsis infans* and the crab *Pseudothelphusa jouyi*, both widely distributed along the middle portion of the Neovolcanic Axis at altitudes between 1500 and 1900 m. This distributional pattern could be the result of an older distribution within the area and the subsequent gradual emergence of the Neovolcanic Axis during the Oligocene and the Miocene. It is interesting that neither *P. infans* nor *P. jouyi* produced more species within their ranges, even though these areas have been repeatedly fragmented. A third group, distributed to the south of the Neovolcanic Axis, comprises the remaining 14 species of *Poeciliopsis* and 22 species of crab.

Generalized track III, South Mexico–Guatemala, is supported by species of the three taxa analysed herein. Fishes are represented by *Poeciliopsis hnilickai*, which is endemic to streams in the Sierra Madre de Chiapas. Several species of crabs of the genus *Tehuana*, although with reduced distribution

areas, constitute a very characteristic element of the freshwater habitats in the region, mainly in the Papaloapan–Jalcomulco basin. With regards to the angiosperms, *Nymphaea conardii* is an endemic species from southern Mexico.

The South Mexico–Guatemala track corresponds to the southern limit of the Nearctic biota, where the Pacific and the Mountain Mesoamerican generalized tracks come together. It is in the Tehuantepec Isthmus where a track bifurcation is seen, with one branch extending towards Oaxaca and Chiapas, and the other one covering Veracruz–Tabasco. Geologically, the Isthmus is a very complex zone (Ferrusquía–Villafranca, 1993), where major tectonic events, such as sea-level changes and continental uplift, have created small isolated basins within a very large plain (De Cserna, 1989). Sea-level oscillations during the Miocene allowed intermittent communication among the hydrological basins, enabling the Neotropical biotic component to extend over both slopes of Mexico (Myers, 1966; Coney, 1982; Rosen, 1985). Within the state of Veracruz, the generalized track goes beyond Punta del Morro, where Contreras *et al.* (1996) find an important biogeographical discontinuity marking a sharp transition between Nearctic and Neotropical fishes. The results of Contreras *et al.* (1996) coincide with those of Pérez-Higareda & Navarro (1980) for reptiles and mammals, and Mulcahy & Mendelson (2000) and Savage & Wake (2001), who found the Coatzacoalcos river basin, south of Punta del Morro, to have the same effect on the amphibian fauna. These data confirm the importance of the Tehuantepec Isthmus as a bifurcation zone that has 'directed' the Neotropical lowland fauna towards coastal environments.

Croizat (1976) considered the Tehuantepec Isthmus to be an important biogeographical zone, where major changes in the distributional patterns of many groups occur. Thus, it might be expected that several nodes connecting generalized tracks will be found in this area. In contrast, other areas, such as the Tarcoles river basin in Costa Rica, which do not have the complex history of the Tehuantepec Isthmus, present nodes (Kohlmann & Wilkinson, 2001; Morrone, 2001b) for Scarabaeinae beetles, because of the confluence of the Mexican Pacific and the West Panama Isthmus provinces. Both provinces could be considered as generalized tracks given the number of endemic species they hold, in the sense that generalized tracks are analogous to areas of endemism (Morrone, 2001a). Therefore the Nicoya–Tonosí basins located in Central America, with four endemic species of *Poeciliopsis*, namely *P. elongata*, *P. maldonadoi*, *P. paucimaculata* and *P. retropinna*, do not correspond to a node in a strict sense, but they are located close to the biogeographical limit proposed by Morrone (2001b) and Kohlmann & Wilkinson (2001), suggesting that the distribution of *Poeciliopsis* in Central America may be the result of a vicariant event. Furthermore, if we rely on the systematics of the group, we can see that *Poeciliopsis* has two subgenera, *Poeciliopsis* and *Aulophallus*, with the latter distributed exclusively in Central America. Probably, the complex tectonic history of Central America (Myers, 1966; Coney, 1982; Rosen, 1985) influenced the

evolution of both *Poeciliopsis* subgenera, a hypothesis that is supported by a molecular phylogenetic analysis (Mateos *et al.*, 2002).

In conclusion, the Mountain Mesoamerican generalized track (Halffter, 1987) runs between 2000 and 3000 m, whereas the Tropical Mesoamerican generalized track (Morrone & Márquez, 2003) includes lowlands, between 500 and 2000 m. In comparison, tracks I and II of this study are located below 1000 m, with basically Neotropical species, whereas the Mountain Mesoamerican and the Tropical Mesoamerican generalized tracks include Neotropical and Nearctic species (Halffter, 1987; Morrone & Márquez, 2003). Furthermore, many of the patterns detected herein for *Poeciliopsis*, pseudohelphusid crabs and aquatic angiosperms are congruent with those for terrestrial taxa, such as amphibians and reptiles (Flores-Villela & Goyenechea, 2003), birds (Escalante-Pliego *et al.*, 1993), and mammals (Ramírez-Pulido & Müdspacher, 1978). This coincidence seems to indicate that common geobiotic processes have induced these patterns.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from <http://www.Blackwell-Synergy.com>:

Appendix S1 Data matrix of taxa (columns) \times hydrological basins (files) analysed by parsimony analysis of endemism (PAE).