Fundamental biogeographic patterns across the Mexican Transition Zone: an evolutionary approach

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Transition zones, located at the boundaries between biogeographic regions, represent events of biotic hybridization, promoted by historical and ecological changes. They deserve special attention, because they represent areas of intense biotic interaction. In its more general sense, the Mexican Transition Zone is a complex and varied area where Neotropical and Nearctic biotas overlap, from southwestern USA to Mexico and part of Central America, extending south to the Nicaraguan lowlands. In recent years, panbiogeographic analyses have led to restriction of the Mexican Transition Zone to the montane areas of Mexico and to recognize five smaller biotic components within it. A cladistic biogeographic analysis challenged the hypothesis that this transition zone is biogeographically divided along a north-south axis at the Transmexican Volcanic Belt, as the two major clades found divided Mexico in an east-west axis. This implies that early Tertiary geological events leading to the convergence of Neotropical and Nearctic elements may be younger (Miocene) than those that led to the east-west pattern (Paleocene). The Mexican Transition Zone consists of five biogeographic provinces: Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, and Chiapas. Within this transition zone, at least four cenocrons have been identified: Paleoamerican, Nearctic, Montane Mesoamerican, and Tropical Mesoamerican. Future studies should continue refining the identification of cenocrons and the reconstruction of a geobiotic scenario, as well as integrating ecological biogeographic studies, to allow a more complete understanding of the patterns and processes that have caused the biotic complexity of this transition zone.

Transition zones are located at the boundaries between biogeographic regions or realms (Darlington 1957), and represent events of biotic "hybridization", promoted by historical and ecological changes that allowed the mixture of different cenocrons (Morrone 2009). They deserve special attention, because boundaries between biogeographic regions are not static lines, but rather areas of intense biotic interaction (Ruggiero and Ezcurra 2003). The Mexican Transition Zone is a complex area where Neotropical and Nearctic biotas overlap, from the southwestern USA to Mexico and part of Central America, extending south to the Nicaraguan lowlands (Darlington 1957, Halffter 1962, 1964, 1972, 1974, 1976, 1978, 1987). Several authors have recognized the special status of this transitional biota from different perspectives. In recent years, several studies have been published under an implicit evolutionary biogeographic approach focused on this interesting area. I integrate these studies into a coherent framework that helps explain the biotic evolution of the Mexican Transition Zone.

During the 19th and 20th centuries, biogeographers debated the mechanisms underlying biotic evolution, but in recent years some authors have concluded that both dispersal and vicariance are relevant processes (Brooks and McLennan 2001, Morrone 2009). Under favorable climatic and geographic conditions are favorable, organisms actively expanded their geographic distribution according to their dispersal capabilities, acquiring what we now view as their ancestral distribution (the role of dispersal). When the organisms have occupied all the available space, their distribution may stabilize, allowing the isolation of populations in different sectors of the area, and the differentiation of new species through the appearance of geographic barriers (the role of vicariance). To analyze the resulting complex patterns, biogeographers need to define specific questions and determine the most appropriate methods to answer them; importantly, this should be integrated within a coherent framework.

Evolutionary biogeography integrates distributional, phylogenetic, molecular, and paleontological data to discover biogeographic patterns and assess the historical changes that have shaped them. It follows five steps (Fig. 1), each corresponding to particular questions, methods, and techniques (Morrone 2009). Panbiogeography and methods for identifying areas of endemism are used to identify biotic components, which are the basic units of evolutionary biogeography. Cladistic biogeography uses phylogenetic data to test the historical relationships between these biotic components. Based on the results of the panbiogeographic
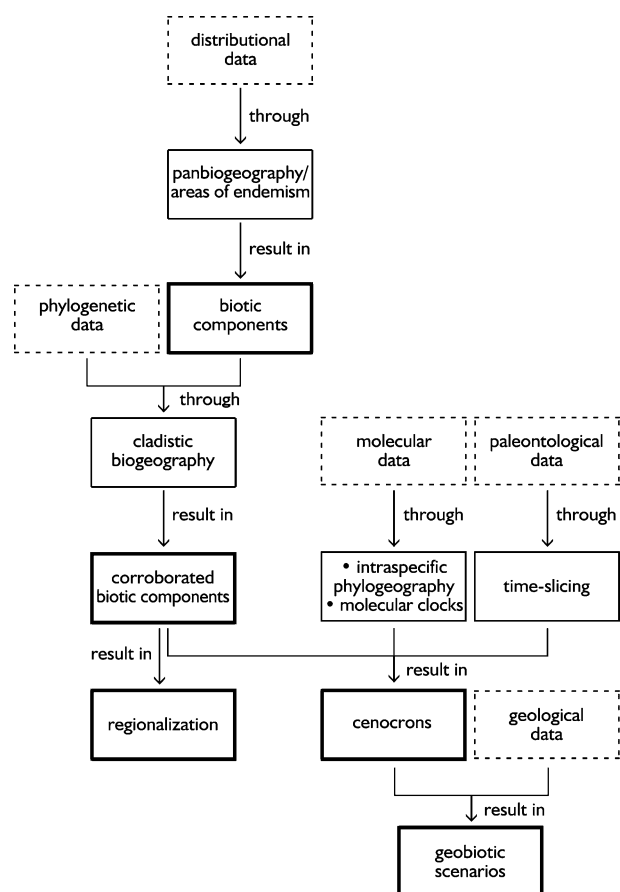
Figure 1. Steps of an evolutionary biogeographic analysis (Morrone 2009).

and cladistic biogeographic analyses, a regionalization or biogeographic classification may be achieved. Intraspecific phylogeography, molecular clocks, and fossils may be incorporated to help identify the different cenocrons that become integrated in a biotic component. Finally, the geological and biological knowledge available can be integrated to construct a geobiotic scenario that may help explain the way the biotic components analyzed evolved. This approach does not imply that every biogeographer must follow all the steps, but that anyone may articulate a specific biogeographic question and choose the most appropriate method to answer it, and given some time, as the different analyses accumulate, coherent theories are formulated by their integrating. This approach, framed under integrative pluralism (Mitchell 2002), does not imply an eclectic or ''anything goes'' approach, but rather that the different methods give partial solutions when answering particular questions.

Within the Mexican Transition Zone, there are studies corresponding to the five steps, which I examine and briefly discuss herein.

Identification of biotic components

Biotic components are sets of spatio-temporally integrated taxa that coexist in given areas. During the 20th century, several authors recognized biogeographic provinces for Mexico (Smith 1941, Goldman and Moore 1945, Cabrera and Willink 1973, Rzedowski 1978, Casas-Andreu and Reyna-Trujillo 1990, Ferrusquía-Villafranca 1990, Ramírez-Pulido and Castro-Campillo 1990, Rzedowski and Reyna-Trujillo 1990), which can be considered preliminary as biotic components. Recent panbiogeographic analyses have tested these components and analyzed their interrelationships.

Morrone and Márquez (2001) analyzed 134 beetle (Coleoptera) species, documenting both a northern and a southern generalized track (Fig. 2A). The former comprised montane areas (Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre del Sur), while the latter included the Sierra Madre de Chiapas and lowland areas in Chiapas, the Mexican Gulf, and the Mexican Pacific Coast, reaching south to the Isthmus of Panama). The northern track included the highest latitudinal and altitudinal mixture of Nearctic and Neotropical cenocrons, with a major Nearctic influence at higher altitudes and a higher Neotropical influence at lower altitudes. Owing to its mixed biota and its placement between the other regions, this generalized track has been considered to represent the Mexican Transition Zone in the strict sense (Morrone 2005, 2006). A previous study, based on mammals (Ortega and Arita 1998), arrived at similar conclusions.

Escalante et al. (2004) analyzed the distributional patterns of 46 Mexican land mammal species belonging to the Nearctic biotic component to determine the southernmost boundary of the Nearctic region in the Mexican Transition Zone. They obtained six generalized tracks (Fig. 2B). The California generalized track lies in the northern part of the California Peninsula, in the state of Baja California, occupying the northern Sierras of Baja California, in the Sierra de San Pedro Mártir, Sierra de Juárez, and the northwestern coastal chaparral. The Center-Gulf generalized track crosses from northern Hidalgo and Veracruz, to southern Veracruz, Puebla, Tlaxcala, and the state of Mexico. The Center-North Pacific generalized track is represented by species distributed on the Sierra Madre Occidental and the Transmexican Volcanic Belt, crossing Durango, Jalisco, Michoacán, and the state of Mexico. The Center-South Pacific generalized track begins in southern Sinaloa, crosses Nayarit, Jalisco, and Michoacán, where it bifurcates: one part crosses the states of Mexico, Puebla, and Oaxaca, and ends in Chiapas, while the other crosses the southwestern portion of the state of Mexico and Guerrero, ending in western Oaxaca. The Isthmus of Tehuantepec generalized track begins in Guerrero and Veracruz, in both the Pacific and Gulf coasts, both parts join in Oaxaca, and then continue to Chiapas. The Chiapas generalized track lies in the Altos de Chiapas pine-oak and tropical montane cloud forests. Intersection of these six generalized tracks led Escalante et al. (2004) to identify nine nodes (Fig. 2B): three in the Transmexican Volcanic Belt, one in the southern Sierra Madre Oriental, one in the eastern Sierra Madre del Sur, one in the highlands of Chiapas, and three in the boundaries between two provinces. They concluded that taxa isolated in the highlands of Chiapas (as well as Guatemala) at the end of the Pleistocene may represent the southernmost Nearctic relicts in Mesoamerica, and that the other biogeographic provinces, together with the Sierra
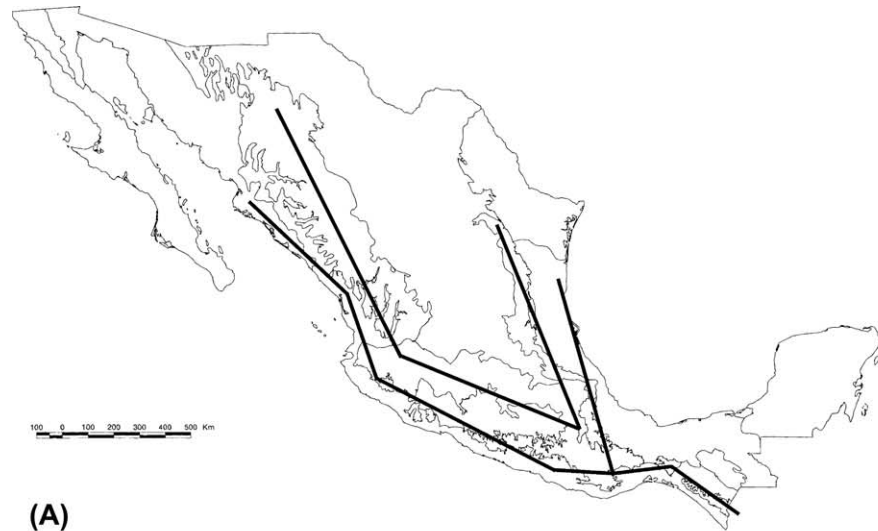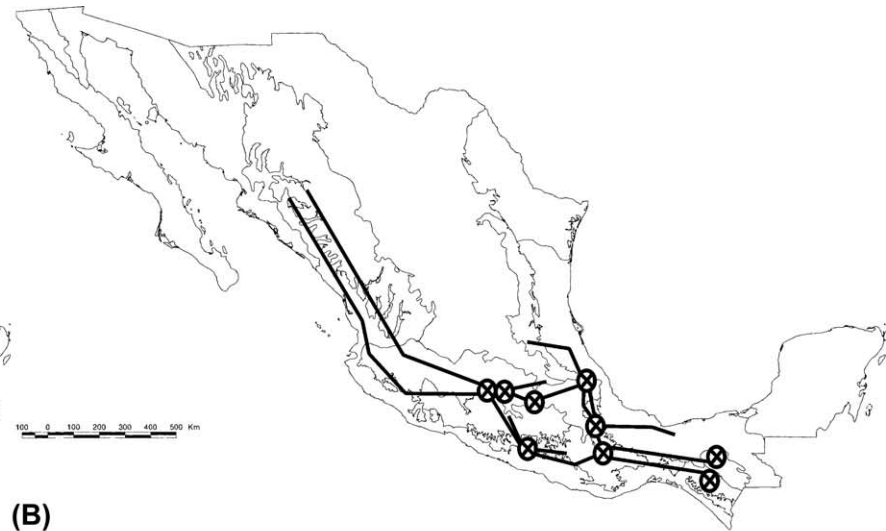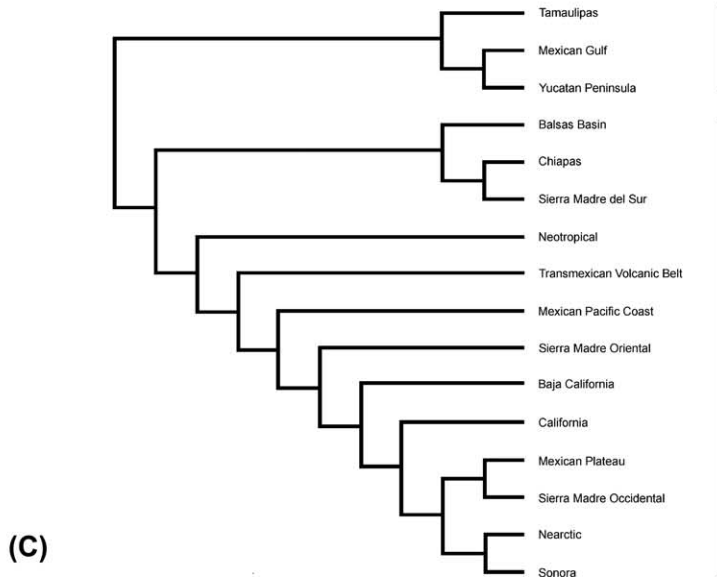
Figure 2. (A) two generalized tracks identified by Morrone and Márquez (2001); (B) six generalized tracks and nine nodes identified by Escalante et al. (2004); (C) general area cladogram obtained by Escalante et al. (2007); (D) provinces of the Mexican Transition Zone. chi, Chiapas; smoc, Sierra Madre Occidental; smor, Sierra Madre Oriental; sms, Sierra Madre del Sur; tvb, Transmexican Volcanic Belt.

Madre Occidental and Balsas Basin provinces, represent the Mexican Transition Zone in the strict sense.

Several other studies have contributed to the recognition of similar generalized tracks and nodes, and to the identification of smaller generalized tracks (Luna-Vega et al. 1999, 2000, 2001, Morrone et al. 1999, Morrone and Escalante 2002, Escalante et al. 2003, 2005, Márquez and Morrone 2003, Ochoa et al. 2003, Morrone and Gutiérrez 2005, Espinosa et al. 2006, Contreras-Medina et al. 2007a, Mariño-Pérez et al. 2007, Toledo et al. 2007, García-Marmolejo et al. 2008).

Testing relationships among biotic components

Once biotic components have been identified, they can be tested using cladistic biogeographic analyses. Some authors have provided cladistic biogeographic analyses of Mexico (Liebherr 1991, 1994, Marshall and Liebherr 2000, Flores Villela and Goyenechea 2001, Espinosa et al. 2006, Contreras-Medina et al. 2007b).

Escalante et al. (2007) analyzed 40 plant and animal taxa distributed in Mexico and extending to both the Nearctic and Neotropical regions. Each taxonomic cladogram was transformed into a taxon-area cladogram by replacing its terminal taxa with the areas in which they occur. A paralogy-free subtrees analysis (Nelson and Ladiges 1996) allowed the construction of a general area cladogram (Fig. 2C), which showed two main clades. The Mexican Gulf, Tamaulipas, and Yucatan provinces are included in one clade, which forms the lowland region of eastern Mexico along the Caribbean coastline as far north as southern USA, possibly extending to Florida. The other clade includes the remaining provinces of central and western Mexico. The eastern boundary of the second clade – the Sierra Madre Oriental, the Sierra Madre del Sur and Chiapas – confines the provinces of the first clade. Within the second clade, a subclade consisting of the Balsas Basin, Chiapas, and Sierra Madre del Sur provinces principally forms the montane areas south of the Transmexican Volcanic Belt. This analysis challenges the commonly held opinion that Mexico is biogeographically divided along a north-south axis, as both main clades divide the country in an east-west axis.

Escalante et al. (2007) concluded that the oldest east-west division found did not contradict the currently recognized north-south axis that roughly divides Mexico into northern and southern portions on both sides of the Transmexican Volcanic Belt. The newly recognized biogeographical divide implies that early Tertiary geological events leading to the convergence of Neotropical and Nearctic elements in the Mexican Transition Zone may be younger (Miocene) than those that led to the east-west pattern (Paleocene). Additionally, the first clade may be recognized formally as a Caribbean region, separate from both the Neotropical and Nearctic regions, which may represent an older region that has existed independently since the Paleozoic. Previous biotic diversification studies of the Mexican Transition Zone need to be revised, because the division between the Nearctic and Neotropical regions in fact incorporates two biotic divisions, a north-south from the Miocene, and an east-west from the Paleocene. Given

the composite biotic nature of the Mexican Transition Zone, a complex pattern was expected to emerge; however, the results showed a single general area cladogram, with an east-west divide instead of the classical north-south division, implicit in previous explanations such as the Great American Biotic Interchange.

Regionalization

Corroborated biotic components may be ordered hierarchically and used to provide a biogeographic classification. The current regionalization of Mexico (Morrone 2001, 2005, 2006) recognizes 14 biogeographic provinces: California, Baja California, Sonora, Mexican Plateau, Tamaulipas, Yucatán Península, Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, Sierra Madre del Sur, Mexican Pacific Coast, Mexican Gulf, and Chiapas. Morrone (2005, 2006) assigned the Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre del Sur provinces to the Mexican Transition Zone. Escalante et al. (2004) argued that Chiapas could be added to the Mexican Transition Zone, and Espinosa-Organista et al. (2008) considered the Balsas Basin to belong to the Neotropical region. The five biogeographic provinces of the Mexican Transition Zone (Fig. 2D), mainly recognized by species of plant and animal taxa (Morrone 2001), are as follows: 1) Sierra Madre Occidental province. Western Mexico, in the states of Chihuahua, Durango, Zacatecas, Sonora, Sinaloa, Nayarit, and Jalisco, above 1000 m altitude. This province has the highest Nearctic influence. 2) Sierra Madre Oriental province. Eastern Mexico, in the states of San Luis Potosí, Coahuila, Hidalgo, Nuevo León, Veracruz, Puebla, and Querétaro, above 1500 m elevation. Biogeographic districts within the Sierra Madre Oriental province have been recognized by Espinosa-Organista et al. (2004). 3) Transmexican Volcanic Belt province. Central Mexico, in the states of Guanajuato, Mexico, Distrito Federal, Jalisco, Michoacán, Puebla, Oaxaca, Tlaxcala, and Veracruz. Biogeographic districts within the Sierra Madre Oriental province have been recognized by Torres Miranda and Luna Vega (2006). 4) Sierra Madre del Sur province. South central Mexico, from southern Michoacán to Guerrero, Oaxaca, and part of Puebla, above 1000 m altitude. 5) Chiapas province. Southern Mexico, Guatemala, Honduras, El Salvador, and Nicaragua; basically corresponds to the Sierra Madre de Chiapas, from 500 to 2000 m altitude.

Identification of cenocrons

After establishing and testing the biotic components, time-slicing, intraspecific phylogeography, and molecular clocks can help establish when the cenocrons assembled within them. Cenocrons are sets of taxa that share the same biogeographic history, which constitute identifiable subsets within a biotic component by their common biotic origin and evolutionary history. From the aforementioned studies, it is evident that the complex biota of the Mexican Transition Zone consists of several cenocrons. Halffter's

(1987) distributional patterns – based on species distributions, their closest relatives, species richness, degree of species sympatry, geological history, and diversity of habitats occupied (Liebherr 1991, 1994) – may be considered as cenocrons (Morrone 2005).

The Montane Mesoamerican cenocron includes Neotropical taxa that evolved in situ in humid montane habitats throughout Mexico and Central America. They have their highest species diversity in Central America, with species in the tropical and cloud forests in the mountains of Oaxaca, and further north and west along the Atlantic and Pacific watersheds. They have South American affinities and are hypothesized to have diversified in the Mexican Transition Zone in the Oligocene.

The Paleoamerican cenocron includes Neotropical taxa that are restricted to Mexican montane areas, with ecological preferences for deserts, grasslands, and rain forests; they may also have some species in Central America. Their closest relatives are Old World temperate and tropical taxa. They underwent diversification prior to the Pliocene closure of the Isthmus of Tehuantepec.

The Nearctic cenocron includes taxa that diversified in the mountains of Mexico during the Pliocene-Pleistocene. The Isthmus of Tehuantepec basically constitutes their southern limit, but these taxa may have a few species in Central America. Taxa generally occupy temperate conifer forests and grasslands above 1700 m of elevation. Their closest relatives are found further north, in the Nearctic region, along the Rocky Mountain Cordillera and areas across the USA and Canada.

The Tropical Mesoamerican cenocron includes Neotropical taxa that evolved in humid lowland habitats throughout Mexico and Central America. They have South American affinities and are hypothesized to have diversified in the Mexican Transition Zone more recently than the taxa assigned to the other cenocrons, in the Pleistocene.

Several recent phylogeographic and molecular clock studies of taxa from the Mexican Transition Zone (Sullivan et al. 1997, 2000, Cuenca et al. 2003, García-Moreno et al. 2004, Becerra 2005, Hasbun et al. 2005, Mateos 2005, Wuster et al. 2005, León-Paniagua et al. 2007) may help refine previously identified cenocrons. These analyses can be used to identify cenocrons and determine how and when they have dispersed and integrated.

Construction of a geobiotic scenario

Once biotic components and cenocrons have been identified, it is possible to construct a geobiotic scenario. By integrating biological and non-biological data, a plausible scenario can be developed to explain the episodes of vicariance/biotic divergence and dispersal/biotic convergence that have shaped biotic evolution. The east-west pattern detected by Escalante et al. (2007) corroborates the geological reconstructions of the Palaeocene to Miocene terrane migration and may help explain Mexican biotic complexity (Iturralde-Vinent 1998, Kerr et al. 1999). The collision of the Caribbean migrating plate 60 Ma predates the beginnings of the 49 Ma North-South American plate convergence, the latter event triggering the Great American Biotic Interchange during the Oligocene (ca 30 Ma) to

Miocene. Currently there is a geophysical debate over the origin and migration of the Caribbean plate since the late Mesozoic (Kerr et al. 1999, Müller et al. 1999). The "Pacific model" states that the Caribbean plate originated in the Pacific Ocean and gradually moved eastward, passing between the North and South American plates prior to collision during the Miocene, into its present position (Kerr et al. 1999). The Caribbean plate may have carried in an evolving biota that remained isolated during the migration. This might explain the existence of a unique and older Caribbean biota that shares complex relationships with both Neotropical and Nearctic biotas.

Other geological events, especially as related to the development of the Sierras Madre and the volcanism of the Transmexican Volcanic Belt (Ferrusquía-Villafranca 1993, Ferrusquía-Villafranca and González-Guzmán 2005), are relevant to explain the vicariant events that led to in situ differentiation within the Mexican Transition Zone (Morrone 2005). Given the Miocene age (ca 15 Ma) of the Transmexican Volcanic Belt, it seems very likely that the split between both subclades is a result of intense volcanic activity that led to a geographical barrier between northern and southern highland provinces.

Discussion

Future studies should continue refining the identification of biotic components and cenocrons and the reconstruction of a geobiotic scenario. Biogeographic regionalization of the Mexican Transition Zone should include more detailed analyses, especially to recognize biogeographic districts within the provinces. The complex biota of the Mexican Transition Zone should be dissected more thoroughly, by analyzing more taxa (especially non-insect invertebrates) from different methodological perspectives.

On the other hand, I believe that integration of ecological biogeographic studies will allow a more complete understanding of the patterns and processes that have caused the biotic complexity of this remarkable transition zone. Ecological models might be particularly useful in providing clues to understand the biotic diversification in the Mexican Transition Zone. In special, island biogeography (Whittaker and Fernández-Palacios 2007) contains models and theories that may be applied to biotic components, which can be treated as islands.

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