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Comparative phylogeography of *Oryzomys couesi* and *Ototylomys phyllotis*: historic and geographic implications for the Central America conformation

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Abstract. Central America is an ideal region for comparative phylogeographic studies because of its intricate geologic and biogeographic history, diversity of habitats and dynamic climatic and tectonic history. The aim of this work was to assess the phylogeography of two rodents codistributed throughout Central America, in order to identify if they show concordant genetic and phylogeographic patterns. The synopsis includes four parts: (1) an overview of the field of comparative phylogeography; (2) a detailed review that describes how genetic and geologic studies can be combined to elucidate general patterns of the biogeographic and evolutionary history of Central America; and a phylogeographic analysis of two species at both the (3) intraspecific and (4) comparative phylogeographic levels. The last incorporates specific ecological features and evaluates their influence on the species' genetic patterns. Results showed a concordant genetic structure influenced by geographic distance for both rodents, but dissimilar dispersal patterns due to ecological features and life history.

Keywords. climate, genetic diversity, geology, Middle America, Muridae

Introduction

Over the past century, Central America (CA) has been recognized as a geographic region with highly complicated geology and climate dynamics, in which processes like speciation, extinction and diversification gave rise to a variety of multiscale genetic and phylogeographic patterns. To understand those patterns, biogeographers have incorporated in their analyses methods developed for the field of intraspecific and comparative phylogeography (CP). Comparative phylogeographic studies rely on the assumption that the most parsimonious explanation for concordant phylogeographic patterns among different species is that they arise because of a shared biogeographic or evolutionary history (Bermingham and Martin 1995, Avise 2000, Arbogast and Kenagy 2001). To test this assumption, CP studies evaluate species that have a shared distribution; for example many species are codistributed along CA and, consequently, likely have been affected by similar geologic and biogeographic processes that defined much of their evolutionary history. As a result, CP studies have found concordant phylogeographic patterns, but also cases where species show dis-

tinct phylogeographic patterns, suggesting that ecology and life history traits, among others, also explain the genetic distribution observed (Sullivan et al. 2000).

Oryzomys couesi and *Ototylomys phyllotis* are rodents that are codistributed in Central America. *O. couesi* ranges from Colombia throughout CA to northern Mexico along the Pacific, the Gulf of Mexico and the Caribbean coasts, while *O. phyllotis* occurs in a smaller area, from Costa Rica to the Isthmus of Tehuantepec (Figure 1). These species have different habitat preferences and ecological characteristics (Lawlor 1982, Reid 1997). Few studies about these species exist, their genetics having been used mainly to describe the phylogenetic relationships of major rodent groups (i.e., Stepan et al. 2004, Reeder et al. 2006, Weksler 2006) and population genetics at local scales (for *O. couesi* only; i.e., Vega et al. 2007). Accordingly, the main objectives of this work were to evaluate the intraspecific and comparative phylogeographic patterns of the two rodent species and assess if they have a concordant phylogeographic response to their shared geologic and climatic history. The influence of their eco-

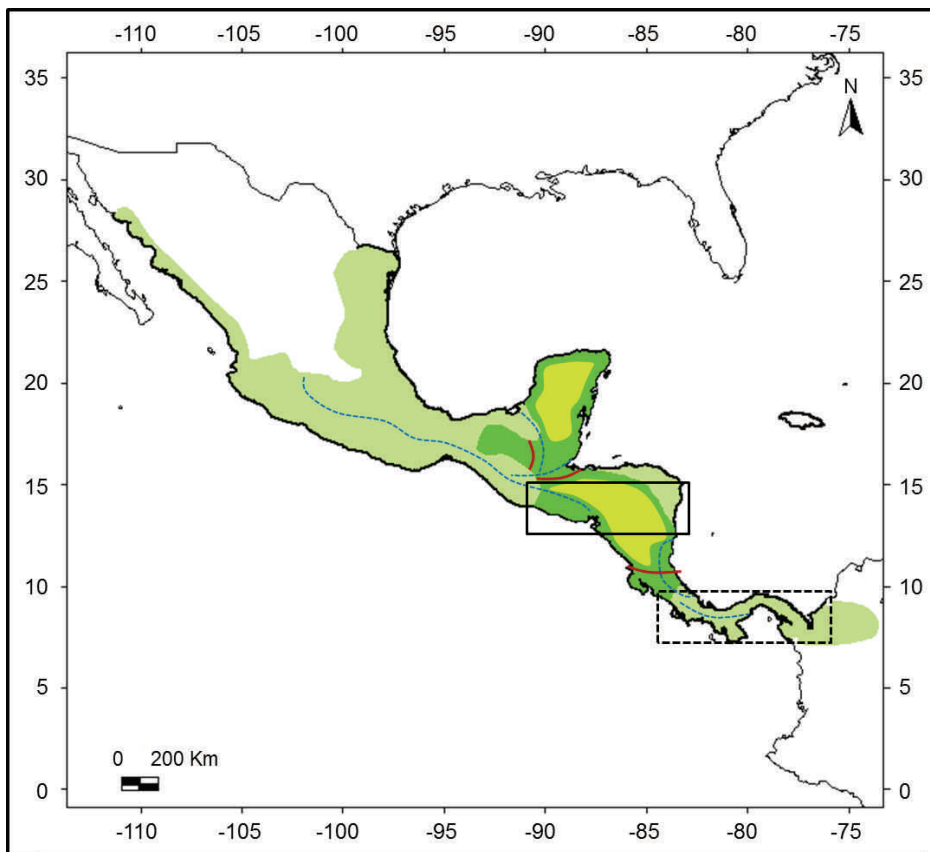


Figure 1. Scheme of distribution and phylogeographic barriers of *Oryzomys couesi* and *Ototylomys phyllotis*. The pale green, dashed blue lines and dashed square are used for *O. couesi*, while the intense green, solid red lines and solid square are used for *O. phyllotis*. The yellow regions show where are located the phylogroups shared among species, the lines indicate the main barriers (climatic and/or geological) associated with the conformation of the major phylogroups and squares indicate the area of origin of each species according to this study.

logical characteristics on the patterns observed was also assessed.

Materials and Methods

Study System

The first two chapters of Gutiérrez-García (2013) are published reviews, one that focuses on the development of the field of comparative phylogeography (CP) and the evolution of the methods used for its analyses (Gutiérrez-García and Vázquez-Domínguez 2011) and the other that defines how genetic and geologic studies can be combined to elucidate general patterns of the biogeographic and evolutionary history of Central America (CA) and of its biota (Gutiérrez-García and Vázquez-Domínguez 2013). Gutiérrez-García and Vázquez-Domínguez (2011) describes the characteristics that shape a CP study, and summarizes the field's primary theoretical, methodological, and analytical requirements, frequent hypotheses tested, and current achievements and limitations, including a variety of illustrative examples throughout. Gutiérrez-García and Vázquez-Domínguez (2013) describes the geologic and tectonic evolution of CA, from the gradual emer-

gence of the area as an archipelago until the emergence of the Isthmus of Panama and formation of CA as a continuous landmass. It follows with the account of the species exchange between North/South America and CA as: a first migration during the Late Cretaceous-Early Paleocene, a second through a terrestrial corridor preceding the formation of the Isthmus of Panama (IP), and the third involving a major dispersion through the IP. Finally, it illustrates how such events, together with the geologic history, caused similar genetic differentiation patterns and left a signature on the diversification of the taxa distributed along this region.

Phylogeographic Analyses

The third chapter of Gutiérrez-García (2013) is the study of the geographic distribution and genetic diversity of *O. phyllotis* based on 132 sequences of a fragment of cytochrome *b* (Gutiérrez-García and Vázquez-Domínguez 2012). It includes a diverse array of phylogeographic tools and analyses to describe the evolution of the species to its present distribution, including the different diversification, dispersal and geologic patterns involved.

Finally, the fourth chapter of Gutiérrez-García (2013) describes the phylogeography of *O. couesi* and focuses mainly on the comparison between the phylogeographic patterns of both species. With this purpose, 201 sequences of a cytochrome *b* fragment of *O. couesi* were analyzed and the phylogeographic patterns determined in much the same way as for *O. phyllotis*. Next, the haplotypes from within the area of codistribution of the two species were grouped based on the following criteria: (1) morphology, (2) geographic and genetic distances, (3) phylogenetic groups, i.e., clades obtained with maximum likelihood and Bayesian phylogenetic estimators, and (4) considering 19 environmental variables (BIOCLIM) and altitude values. These groups were analyzed with different genetic and multivariate statistics in order to test which of four hypotheses (morphological, phylogeographic, phylogenetic and ecological) more significantly explain the genetic structuring of the species (i.e., different lineages).

Results

Ototylomys phyllotis showed high to moderate genetic diversity, with three major phylogeographic lineages whose distribution coincides with the main geological features that shaped Middle America. The origin of the genus was before 3.35 ± 0.21 million years ago (Myr), prior to the Great American Biotic Interchange (GABI), and its initial occurrence was near the centre of its current distribution (Honduras/El Salvador, Fig. 1), from which it later spread (3.20 ± 0.19 Myr) following a series of GABI pulses (Gutiérrez-García and Vázquez-Domínguez 2012). *Oryzomys couesi* has an origin in southern Central America (Fig. 1), also with high to moderate genetic diversity values, and is divided into seven phylogeographic groups. Out of the total number of phylogroups, the two species coincide only in the conformation of two, one located in Central America (Honduras, Guatemala, Nicaragua and Costa Rica) and one located along the Yucatan peninsula in southern Mexico. Additionally, both species show demographic signatures of population expansion, but potential bottlenecks are sug-

gested for some *O. phyllotis* phylogroups. Multivariate analysis indicated that genetic structure between lineages is significantly associated with the phylogeographic hypothesis for both species, while structure at the level of populations within lineages is explained by the ecological (*O. couesi*) and morphological (*O. phyllotis*) hypotheses. Finally, ecological variables are significantly associated with structure at the level of individuals within populations. Precipitation was the primary significant ecological variable for both species, although altitude and temperature variables were also important for *O. couesi*.

Discussion

The comparative phylogeography of two Neotropical rodents, *O. couesi* and *O. phyllotis*, with overlapping distribution in Mexico and Central America, show that these species have shared their geographic range at least for the past 3 Myr. A 'mixed' phylogeographic response can be described, where both species have concordant patterns for two of the lineages or phylogroups identified for each species: Central America and Yucatan peninsula. These lineages have a genetic and phylogeographic structure influenced by major geologic features and climatic events (mountains, volcanic chains and diverse barriers like the Isthmus of Tehuantepec), together with the emergence of the Isthmus of Panama that triggered the Great American Biotic Interchange. The dispersal and diversification of both rodents are tightly linked to the geologic and climatic history of the region, with extremely high genetic diversity occurring throughout the entire range, the highest of which was in the Yucatan peninsula, where the phylogroups of both species experienced range expansion. Also, at a smaller geographic and evolutionary scale, results showed evidence that genetic structuring of populations is associated with the species' ecological characteristics, identifying some climatic and morphological variables significantly associated with their genetic structures. On the other hand, discordant patterns also were observed: the origin and subsequent dispersal of the two species were not similar (Fig. 1), and their ecological features and species-specific life-history

characteristics resulted in mixed responses to some vicariant events. A study like the present, which involved species with different ecological requirements, origin and life history, codistributed in a biogeographically complex area like Central America, is ideal to test hypotheses about concerted and/or independent phylogeographic responses.

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