Revista Mexicana de Biodiversidad 79: 541- 542, 2008
http://dx.doi.org/10.22201/ib.20078706e.2008.002.544

Nota científica

Parsimony analysis of endemism (PAE) and studies of Mexican biogeography

PAE y el estudio de la biogeografía de México

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Abstract. Parsimony analysis of endemism (PAE) has become a popular analytical approach in efforts to map the biogeography of Mexican biotas. Although attractive, the technique has serious drawbacks that make correct inferences of biogeographic history unlikely, which has been noted amply in the broader literature.

Key words: parsimony analysis of endemism, biogeography, area history.

Resumen. El PAE se ha convertido en un método popular en los esfuerzos por resumir, en forma de mapas, la biogeografía de la biota de México. A pesar de su atractivo, la técnica tiene problemas serios que impiden que las conclusiones resultantes sean las correctas. Estos problemas se han hecho ampliamente evidentes en la literatura sobre este campo.

Palabras claves: PAE, biogeografía, historia de áreas.

Mexico has long been known as a fascinating biogeographic arena, with its complex interplay of Nearctic and Neotropical, montane and lowland, and humid and arid, and as such has drawn the attention of many biogeographers (Ramamoorthy et al., 1993). Over the past few decades, however, Mexico's scientific activity has earned the country appreciation as a region of intense activity in the study of biogeography as well, with intense activity in studies of theory, phylogeny, phylogeography, distribution, and endemism (Halffter, 1987; Sánchez-Cordero, 2001; Pérez-Ponce de León and Choudhury, 2005). A recent fashion, however, has been the development of numerous studies based on the technique termed Parsimony Analysis of Endemism (PAE), which is the focus of this commentary.

PAE is based on admirable goals, to reconstruct area history based on patterns of shared endemic species (Rosen, 1992), without the need for detailed phylogenetic studies of individual lineages. Although the original version of PAE was intended to cross temporal samples, detecting appearance of new species in stratified samples through time (Nihei, 2006), this more static version bases inferences on a matrix of species X sites, and uses cladistic analyses to link areas on the basis of shared endemic species, which are ostensibly analogous to shared derived characters in a phylogenetic analysis. A considerable number of studies of Mexican biogeography using PAE has now accumulated (Morrone and Escalante, 2002; Escalante et al., 2003; Rojas-Soto et al., 2003; Escalante et al., 2005).

PAE, however, has now seen numerous, serious, profound criticisms in the broader biogeography literature (Brooks and van Veller, 2003; Santos, 2005; Nihei, 2006; Santos and Amorim, 2007), which should be taken into consideration by Mexican biogeographers prior to choosing PAE as the method of choice for a particular study. In particular, PAE falls short for reasons including the following:

1. *Rooting PAE trees to an all-zero ancestor*. The practice of rooting the PAE areas tree to a hypothetical ancestor that has all species set to zero (= absent in all areas) requires the implicit assumption that the only relevant processes are of vicariance, and that dispersal plays no role in assembling communities.

2. Non-*endemism is required for insight*. In a perfectly vicariant world, each area would have its own species in each lineage that has spread across the landscape of interest. This situation would create PAE character-state matrices in which each species is autapomorphic for each area, which will prove uninformative in cladistic analyses, and no hypotheses of area relationships will result. As such, PAE is not so much analysis of *endemism* as much

Recibido: 12 febrero 2008; aceptado: 16 mayo 2008

as analysis of *non*-endemism, if areas are to be linked successfully using the PAE approach.

3. *PAE may group areas based on shared absence or shared dispersal*. Because the PAE approach focuses so absolutely on vicariance, any dispersal that is at all nonrandom or directed in any way may produce apparent patterns of shared "derived" species that will be misleading regarding true historical signal. That is, any dispersal corridor, consistent wind or ocean current, or even chance events, that might concentrate dispersal events in certain areas can mislead PAE analyses. PAE groupings can also result from shared absences, and the meaning of a shared non-presence of an endemic species for history of areas is not at all clear.

4. *Not applicable to artificially delimited areas*. PAE is applicable only to closed systems, to which the lineages under analysis should be endemic. Otherwise, some species may occur in areas outside of the area of analysis, but these relationships will not be apparent in the results, as those other areas are excluded from consideration.

The rush to apply PAE to each system of interest in Mexican biogeography has led to some high points and some low points. On the positive side, a few careful analyses have offered useful and valuable insights into PAE and its application (Rojas-Soto et al., 2003); these studies will be useful if and when PAE is to be used in biogeographic studies. The negative side, however, is more worrisome: applications to "Mexican" areas only (Morrone and Escalante, 2002) leave out potentially related areas in neighboring regions. Other recent studies, not published, to my knowledge, have even attempted to apply PAE to presences and absences of *all* taxa, not even limiting analysis to resident species, much less to endemic taxa (pers. observ.)! PAE has become so very popular in Mexican biogeography, I believe, simply because it is so easy to apply, and not because it is the best or even an *appropriate* tool for the job. The long and the short of the situation is that most PAE applications, and particularly those applied to Mexican biotas, have been based on poor assumptions and have used a tool that is unlikely to yield deep insights into biogeography; as such, Mexican biogeographers should think twice before using this approach.

More broadly, and in conclusion, PAE falls short owing in largest part to its absolute focus on vicariance. Dispersal also exists, and is a major structuring force in biogeographic processes, like it or not. Otherwise, species' ranges would only subdivide further and further through time, and biological diversification would only produce more and more micro-scale endemism. In reality, although vicariance is perhaps the most common mechanism of speciation (Barraclough and Vogler, 2000), dispersal acts frequently to ratchet up range sizes, and offer vicariance a broader field of geographic phenomena with which to generate more biological diversity. PAE denies these mechanisms in its reconstructions, and its reconstructions are thereby unreliable and quite suspect.

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