

A performance evaluation of pattern-based and event-based methods of historic biogeography: recovering the historical signal

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RESUMEN: El desempeño de tres metodologías de biogeografía histórica: Parsimonia de Brooks (BPA), análisis de árboles reconciliados (RTA) y análisis de dispersión-vicarianza, fueron analizados en base a su capacidad de reconstruir relaciones de áreas previamente conocidas. Para evaluar el desempeño de los métodos, se emplearon una serie de juegos de datos que contenían diferentes variables (tales como áreas ausentes, clados politómicos, taxas redundantes, relaciones filogenéticas conflictivas y taxas ampliamente distribuidos). Los resultados mostraron que el BPA es el método que asume menos supuestos *ad hoc*, mientras que el RTA fue el método más sensible a la frecuencia de clados que presentaban alguna variables (por ejemplo politomías). Cuando DIVA fue comparado con BPA, no mostró un mejor desempeño basado en el número de eventos vicariantes recuperados. Un análisis con datos empíricos empleando clados de escarabajos (Coleoptera: Carabidae) de Mesoamérica y México fue analizado utilizando el BPA. Un solo cladograma general de áreas fue encontrado con diferencias evidentes al previamente publicado por Liebherr.

PALABRAS CLAVE: BPA, Carabidae, DIVA, Biogeografía histórica, Mesoamérica, RTA.

ABSTRACT: The performance of three different methodologies of historical biogeography, Brook's parsimony analysis (BPA), reconciled tree analysis (RTA) and dispersal vicariance analysis (DIVA), was assessed based on their ability to recover a previously known area relationship. To test the methods a series of theoretical data sets containing different effects (such as missing areas, polytomic clades, redundant taxa, different phylogenetic relationships and widespread taxa) were used to evaluate the performance of BPA, RTA and DIVA. The results found that BPA is the method to invoke less *ad hoc* assumptions; in addition, RTA was found to be more sensitive to the frequency of clades containing an effect (e.g. polytomies). When DIVA was compared with BPA, it did not outperform BPA based on the number of vicariant events recovered by the techniques. Additionally, an empirical analysis using carabid clades (Coleoptera: Carabidae) from Mesoamerica and Mexico was analyzed using BPA, from which a single general area cladogram was obtained showing evident differences with the general area cladogram previously published by Liebherr.

KEY WORDS: BPA, Carabidae, DIVA, Historical Biogeography, Mesoamerica, RTA.

INTRODUCTION

Historical Biogeography has undergone in recent years a scientific revolution concerning its philosophical and methodological foundations; as a consequence nine Historical Biogeography methodological approaches currently can be found in the literature: centers of origin and dispersal (Matthew 1915), panbiogeography (Croizat 1958), phylogenetic biogeography (Brundin 1966), cladistic biogeography (Rosen 1978, Nelson and Platnick 1981) phylogeography (Avise et al. 1987), parsimony analysis of endemism (Rosen 1988), event-based methods (Ronquist 1997), ancestral areas (Bremer 1992), and experimental biogeography (Haydon et al. 1994). According to Crisci (2001) and Morrone and Crisci (1995) these nine approaches embrace approximately 30 different techniques.

Under the Vicariance Biogeography two different methodologies are considered: pattern-based and event-based methods (Ronquist and Nylin 1990, Van Veller 2002, 2003). Pattern-based methods derive divergent patterns or area cladograms based on taxon-area cladograms; in contrast, event-based methods at different biogeographical scenarios are analyzed using cost functions to different biogeographic processes (Ronquist 1997, 1990). Currently, two different approaches are considered in Vicariance Biogeography (Van Veller 2003): the cladistic and the phylogenetic biogeography (*sensu* Van Veller 2003).

Until recently, has been assumed that the methods used under the cladistic and the phylogenetic biogeography were developed to implement the same research program. Conversely, Van Veller et al. (2002) made the distinction between *a priori* and *a posteriori* methods, based on the protocols to derive the area cladograms; *A priori* methods modified the data in order to provide maximum fit of exceptions (sympatric or widespread taxa) to a

single area cladogram. Among the most used *a priori* methods are Reconciled Trees Analysis (RTA, Page 1994) and Component Analysis (Page 1990). In the other hand, *a posteriori* methods do not allow modification of the data and make use of Maximum Parsimony in order to find the general area cladogram; exceptions are explained *a posteriori* as post-speciation dispersals or as speciation by dispersal events. Among the *a posteriori* methods can be found the Brooks Parsimony Analysis (BPA, Wiley 1986, Brooks et al. 2001) and the Component Compatibility Analysis (Zandee and Roos 1987).

Among the current diversity of methodologies, the critical issue in the current historical biogeography debate is: which approach is the best? Therefore, the aim of this paper is to evaluate the performance of two methodologies, pattern-based and event-based methodologies, to recover the “true” history of a set of geographical areas. Also, different sets of “effects” (like unresolved relationships among the cladograms used, widespread taxa, sympatric and missing areas) were used to evaluate the performance of the BPA, RTA and DIVA.

METHODS

In order to evaluate the performance of pattern-based methods, two different approaches were used: an *a priori* method (RTA-Component version 2.0, implemented *as is*) and a *a posteriori* method (BPA-NONA). In addition the Dispersal-Vicariance analysis (DIVA, Ronquist 1997) was used as an event-based method for comparison with the *a priori* methods.

The performance of the techniques was estimated at two different levels: 1- based on the recovery of the “true” general area cladogram, and 2- the explanation of the departures from the “true” general area cladogram by each methodology. Also, the

techniques performance was compared using two measurements: the percent of common groups as an estimation of taxonomic congruence (Wheeler 1995), and the number of *ad hoc* assumptions (i.e. extinction, duplication and dispersal events) invoked by the methodologies. For enumerating common groups, the percent of shared groups were employed for which only the groups that are monophyletic in both trees (“true general area cladogram” vs proposed reconstruction) were considered as congruent.

The results acquired from DIVA were evaluated in a different way due to the fact that this technique was made for the study of single clades; therefore, the data sets with polytomies, missing areas and different phylogenetic relationships were not possibly assessed with this method. However, it is possible to compare the number of speciation events explained in terms of vicariance/dispersal events for the three(s) obtained by DIVA vs. BPA.

Two case scenarios were addressed with DIVA: 1- favoring vicariance events, in which the number of ancestral areas was unconstrained, and 2- favoring dispersal events with the number of ancestral areas set to two instead of one (Ronquist 1997, Zink et al. 2000).

Theoretical and empirical data sets

A theoretical data set was constructed with five clades that were present in a complete pectinate tree. Then, series of data matrixes were constructed in which each one of them contained 5 clades, from which one clade presented the factor of interest to be studied (such as polytomies, widespread taxa, sympatric and absent areas). Furthermore, the number of clades containing the factor of interest (in the set of five clades) was evaluated considering two clades instead of just one clade.

The empirical data sets used in this paper consist of taxon area cladograms for the following Carabidae (Coleoptera) genera or species groups: *Loricera* (Ball and Erwin 1969), *Notiobia* (Noonan 1986), *Agonum cyclifer* group (Liebherr 1994b), *Agonum cyanope* clade (Liebherr 1986, 1994b), *Elliptoleus* (Liebherr 1991), *Calathus* (Ball and Negre 1972), *Platynus degallieri* group (Liebherr 1992), *Platynus hamatus* clade (Liebherr 1988), *Phloeoxena megalops* group (Ball 1975), *Eripus* (Straneo and Ball 1989), *Amblygnathus iripennis* group (Ball 1987), *Pelmatellus* (Goulet 1974), *Trichopselaphus* (Ball 1978, 1987), *Euproctinus* (Shpeley 1986), and the genus *Progaleritina* (Ball and Nimmo 1983). Initially, the mentioned genera and species groups were used by Marshall and Liebherr (2000) to estimate the general area cladogram for areas of endemism in Mexico and the Mesoamerican region.

On the current analysis, the same carabid clades used by Liebherr 1994a and Marshall and Liebherr 2000 were employed and analyzed with BPA (see Appendix I for data matrix). The clades were used without any modification, except for the exclusion of the geographical areas outside of the geographical region of interest (i.e. Caribbean, North America).

Evaluation of effects

The following effects were evaluated: polytomies, missing areas (extinction), redundant taxa (sympatric taxa), widespread taxa (dispersal) and different phylogenetic relationships among taxa of the “effect clade” (i.e. non-response to vicariance events) (Appendix I).

Polytomies were included near the base of the clade, in an intermediate position and in the most distal node to evaluate the placement of the polytomies in the general area cladogram. In addition, the clade containing a polytomy at node 51 was evaluated in five analyses, each

one containing an increasing number of clades within the same polytomy. Two additional analyses were performed to evaluate the effect of the number of clades within the polytomy as well as the effect of the polytomy position (basal vs. at tips) within the clade phylogenies.

The effect of missing areas was explored using single clades with one missing area at different places on the area clad phylogeny. Also, tests were conducted in order to study the effect of the number of missing areas for the overall area phylogeny using a clade with two missing areas at different places on the area clad phylogeny.

The effects of redundant taxa were analyzed by placing different taxa with the same area at different places on the clad phylogeny, for a total of four scenarios. Additionally to the clad number effect scenario, a combined scenario between missing areas and redundant taxa was studied (See table 1 and 2 in appendix for details).

Three different clades implying different phylogenetic relationships were used to explore conflicting information over taxon relationships; also, an additional non-pectinate tree was used to assess a complete different set of relationships. DIVA analysis cannot be performed on these data sets, as mentioned above, due to its single case design.

The effect of widespread taxa was evaluated using three clades at different positions on the area phylogenetic tree. In addition, two additional analysis were performed to explore the effect of the number of widespread taxa on the area cladogram phylogeny: 1- one clade with two cases of widespread taxa, 2- one clade with three cases of widespread taxa

RESULTS

The polytomy effect

According to Ronquist (1997) the evaluations of the polytomies were only possible for BPA and RTA because DIVA has not been implemented for unresolved cladograms.

RTA demonstrated to be more sensitive to the number of polytomic clades involved in the data sets. In cases with 60% of polytomic clades in the data set, RTA will not correctly recovered the true general area cladogram (PSG <1 Table 1). On the other hand, BPA will recover the correct area tree topology even with 80% of polytomic clades present in the analysis. In the extreme case at which all clades were polytomic, BPA will show a polytomy as a result.

According to the present results RTA needed to invoke more *ad hoc* events to adjust the clad effect to the true area tree (three to six extinctions and one to two duplications), but the BPA analysis did not required to invoke these *ad hoc* events (Table 2).

Finally, BPA and RTA consistently recover the true general area cladograms despite of the position of the unresolved node in the taxa cladograms. However, RTA required invoking more extinctions events when the polytomies were near the root node (Table 2).

Missing area effect

When BPA and RTA were used to assess the missing areas data sets, both techniques obtained the true general area cladogram (table 1). Both, BPA and RTA, showed 1 or 2 *ad hoc* events of extinction depending on the number of missing areas present in the analysis (Table 2). There were not evidence of poor performance when different missing area positions within the clad where explored.

Sympatric or Redundant taxa effect

The redundant taxa did not showed noticeable effects on the recovery of the general area

cladogram when BPA and RTA were implemented. Even more, the general area cladogram was recovered by both techniques when just one effect taxon was present (PSG=1 Table 1). When two redundant taxa were present, BPA needed just one dispersal event to explain the clade effect into the general area cladogram; conversely, RTA needed to invoke one duplication and 2 to 4 extinctions depending on the redundant taxa position within the area tree topology. Additionally, RTA invoked more *ad hoc* events when three redundant taxa were present when compared with BPA (Table 2).

The DIVA analysis explained 84 to 88% of the speciation events as the result of vicariant events when dispersal events were favored for the two redundant taxa case; while 96 to 100% as vicariant speciation events when vicariance along was allowed in the analysis. On the other hand, BPA explained 96% of the speciation events as the result of vicariant events independently of the scenario tested.

Different relationships effect

The general area cladogram was recovered correctly by the BPA and RTA methods (Table 1), but there were differences between the techniques on the number of *ad hoc* assumptions invoked by the methodologies: BPA required one dispersal event, while the RTA method needed one duplication and between four to six extinctions to explain the obtained cladogram. Also, the number of extinctions events invoked increased as the location of the “effect taxon” was located closer to the root node (Table 2). In a similar way, the number of *ad hoc* events postulated by TRA increases when a non-pectinate tree was analyzed, while BPA required to invoke a lesser number of events than RTA (Table 2).

Widespread taxa effect

Despite of the widespread taxa both methodologies, BPA and RTA, recovered the correct general area cladogram (Table 1). However, BPA required invoking one *ad hoc* dispersal event to explain the widespread distribution of taxa at different positions within the clade. In contrast, RTA needed to invoke one duplication and one to five extinctions for the same scenario. In addition, as a general tendency was observed that if the “effect taxon” is placed closer to the cladogram root, more *ad hoc* extinction events were postulated by the methods, BPA and RTA, to explain the obtained cladogram (Table 2).

On the other hand, when DIVA was used within a scenario favoring vicariance it’s explained 96% of the speciation events as the result of vicariant events. But when DIVA was used within the scenario favoring dispersals, DIVA found 80 to 84% of the speciation events to be the result of vicariant events. In contrast, BPA explained 96% of the events as the result of vicariant events, matching the main mode of speciation implicit in the scenario.

DISCUSSION

In all the instances created to evaluate the recovery of the true general area cladogram BPA and RTA recovered the correct area cladograms; however, RTA showed a mayor sensibility to the number of polytomic clades included in the evaluated data sets. Also, when the effect of clade number was analyzed, BPA showed better recovery of the historic signal (i.e. polytomies) and a better representation as a polytomy at the node of concern. The behavior of RTA is not unexpected, Page (1994) clearly stated that RTA was not implemented to tread polytomic clades, but the possibility of correction for the algorithm exists. Therefore, the effect taxa involved in the polytomies are resolved in an arbitrary way (Page 1990). On the BPA general area cladogram a polytomy will look as a non-response to speciation and a reduction in the

number of taxa supporting the polytomic node. There was an observable effect in the placement “effect taxon” within the taxa cladogram, producing in the methods the invocation of more *ad hoc* assumptions when the “effect taxon” was closer to the cladogram root; this trend was observed in the polytomies, different phylogenetic relationships and widespread taxon data sets analyzed. A possible explanation for the observed trend is that when a conflicting clade within the general area cladogram is placed closer to the tips of the tree, is expected to show more congruence due to a reduction in the number of terminals involved above that particular node. For the data sets with missing areas (extinction events), BPA and RTA did not show any difference in their performance and both recover correctly the general area cladogram. However, when the taxa showed redundant distributions (sympatry) *a posteriori* BPA require to invoke 1 or 2 dispersal events to explain the obtained tree topology. In comparison, RTA used duplications and extinctions to adjust the effect clade to the general area cladogram; the greater number of *ad hoc* events is a consequence of the implementation of the method because RTA sacrifices *a priori* the horizontal transfer in exchange of maximum co-speciation events (Page 1994). The same results were obtained when widespread species were considered as well as different phylogenetic relationships of the species in the general area cladograms.

It is important to point out that RTA can consider *a posteriori* the dispersal events under Assumption 1 (Page 1990, 1994, Van Veller et al. 2000). However, the RTA analysis were currently performed *as is* under Assumption 0; therefore, the lack of dispersal events in the results obtained for this technique. Nevertheless, these same results were obtained by Dowling (2002) when RTA and BPA were compared in their accuracy to recover coevolutionary patterns; in which RTA consistently invoked more *ad hoc* duplication and extinction events, even considering the *a*

posteriori solution for the observed dispersal events (host switches).

In all cases in which the dispersal-vicariance analysis could be implemented, it invoked equal or more instances of dispersal events as explanations for the general area cladogram. In addition, DIVA only considers dispersal as a general category; in contrast, BPA can discriminate among different instances of dispersal, like post-speciation dispersal and speciation by dispersal events (Brooks and McLennan 2001, 2003; Brooks et al. 2001).

Several practical aspects can be concluded from the performed analysis: 1- The technique that invoke the minimum number of *ad hoc* events was BPA, at the same time this technique also recovered the general pattern even when the number of effect clades were significantly increased (e.g. number of wide spread taxa). 2- When single clades are considered DIVA showed in the best case the same result of BPA, however this technique is not correct to the recovery of general patterns (is an event-based method). 3- RTA showed in most of the data sets an exceeding number of duplications and extinctions to reconcile the effect clade to the general pattern. Therefore, considering the results obtained in this paper, BPA appears to be the technique with better historic recovery performance within the scenarios tested.

Study case: The Mesoamerican biogeography

The Mesoamerican region has been considered one of the most species rich regions of the world. This region comprises the geographical area between the Tehuantepec isthmus (at its North limit) to the South area of the Panama isthmus.

Liebherr (1994a) reconstruct the historical relationships among endemic areas for the Mesoamerican and Mexican areas based on carabid species distributions, and the BPA area analysis produced 9 equally parsimonious general area cladograms. After the Liebherr's attempt Hernandez-Baños et al. (1995)

analyzed the region based on montane forest birds distribution patterns.

More recently, Marshall and Liebherr (2000) used the carabid clades plus additional clades from other taxa, to resolve the historical relationships for the endemic areas. The clades were converted from taxon area cladograms into fundamental area cladograms, and then analyzed with a BPA analysis. Their result was a single general area cladogram with two subclades: a northern and a southern clade (Fig 1). Based on their results, Marshall and Liebherr (2000) concluded that Southern Sierra Madre Occidental and Sierra Transvolcanica were included in the southern clade and therefore the south limits of the northern clade was the Sierra transvolcanica instead of the

Isthmus of Tehuantepec. The inclusion of the Sierra Madre Occidental into the southern clade was interpreted as a link established earlier in the developing of the western portions of the Sierra Transvolcanica. The position of Sierra Madre Oriental among the northern endemic areas was found consistent with the hypothesis of a woodland corridor in conjunction with the Sierra Madre Occidental (Van Devender 1990). The position of the Talamanca Cordillera suggested to Marshall and Liebherr (2000) that the vicariant events on the isolations of the other areas, within the southern clade, occurred posterior to its emergence during the Jurassic.

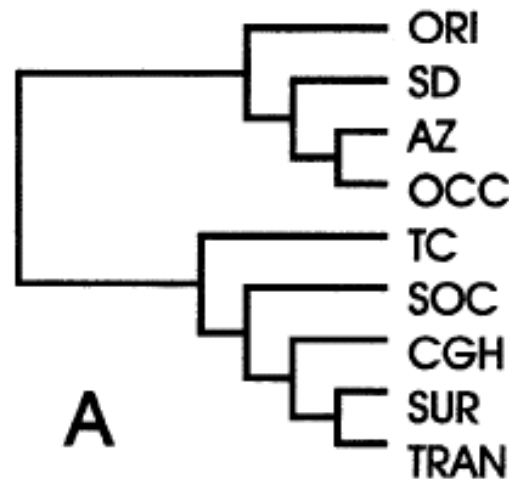


Figure 1. General Area Cladogram obtained by Marshall and Liebherr (2000) as a result of a BPA analysis. ORI: Sierra Madre Oriental; SD: Sonora desert; Az: Arizona; OCC: Sierra Madre Occidental + Central Plateau; TC: Talamanca Cordillera; SC: Southern Sierra Madre Occidental; CGH: Chiapas-Guatemala Highlands; SUR: Sierra Madre Sur, and TRAN: Sierra Transvolcanica.

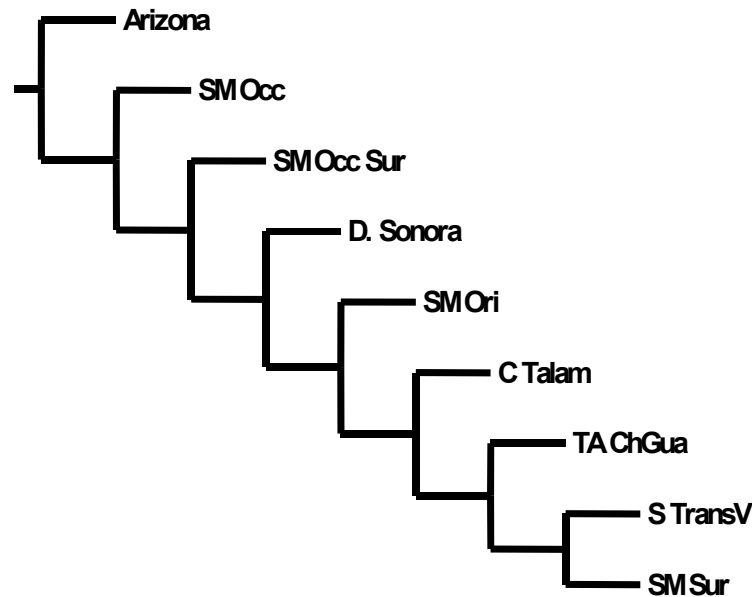


Figure 2. Single General area cladogram obtained by BPA of carabid clades. SMOri: Sierra Madre Oriental; D: Sonora: Sonora desert; Arizona: Arizona; SMOcc: Sierra Madre Occidental + Central Plateau; CTalam: Talamanca Cordillera; TAChGua : Chiapas-Guatemala Highlands; SMOcc SUR: Sierra Madre Occidental Sur; S.TransV: Eje Transvolcanico, and SM Sur: Sierra Madre Sur.

On the current analysis, the carabid clades used by Liebherr 1994a and Marshall and Liebherr 2000 were employed and analyzed with BPA based on its better performance to recovered the general area cladogram (see Appendix I for data matrix). The clades were used without any modification, except for the exclusion of the geographical areas outside of the geographical region of interest (i.e. Caribbean, North America). As results, a single general area cladogram was obtained (Fig. 2), in which none of the northern and southern clades divisions were recovered. Instead, the most basal area recovered was Arizona and a series of vicariant events, from north to south, involving Liebherr' Northern clade areas were recovered. The structure of Liebherr's Southern clade is more or less maintained in the present results with the Talamanca Cordillera as the vicariant event

after which the Chiapas-Guatemalian HighLand, Sierra Transvolcanica and Sierra Madre Occidental Sur endemic areas developed. Therefore, the assertion made by Marshall and Liebherr (2000) on the novel discovery of the Sierra transvolcanica as a limit for the southern endemic areas still holds true.

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REFERENCES

- Awise JC, Arnold J, Ball RM jr., Bermingham E, Lamb T, Niegel JE, Reeb CA , Saunders NC. 1987.** Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review in Ecology and Systematics*, 18, 489-522.
- Ball GE, Erwin TL. 1969.** A taxonomic synopsis of the tribe Loricerini Coleoptera: Carabidae. *Canadian Journal of Zoology*, 47, 877-907.
- Ball GE. 1987.** The Neotropical genus *Trichopselaphus* Chaudoir Coleoptera: Carabidae: Harpalini: new species and a review of taxonomic and evolutionary aspects. *Transactions of the American Entomological Society*, 112, 249-287.
- Ball GE. 1975.** Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir Coleoptera: Carabidae. *Quaestiones Entomologicae*, 11, 143-242.
- Ball GE. 1978.** The species of the Neotropical genus *Trichopselaphus* Chaudoir Coleoptera: Carabidae: Harpalini: classification, phylogeny and zoogeography. *Quaestiones Entomologicae*, 14, 447-489.
- Ball GE. , Maddison DR. 1987.** Classification and evolutionary aspects of the species of the New World genus *Amblygnathus* Dejean, with a description of *Platymetopsis*, new genus, and notes about selected species of *Selenophorus* Dejean Coleoptera: Carabidae: Harpalini. *Transactions of the American Entomological Society*, 113, 189-307.
- Ball GE , Negre J.1972.** The taxonomy of the Nearctic species of the genus *Calathus* Bonelli Coleoptera: Carabidae: agonini. *Transactions of the American Entomological Society*, 98, 412-533.
- Ball GE. , Nimmo AP.1983.** Synopsis of the species of subgenus *Progaleritina* Jeannel, including reconstructed phylogeny and geographical history Coleoptera: Carabidae: *Galerita* Fabricius. *Transactions of the American Entomological Society*, 109, 295-356.
- Bremer K. 1992.** Ancestral areas: a cladistic reinterpretation of the center of origin concept. *Systematic Biology*, 4, 435-445.
- Brooks DR, Van Veller MGP , MacLennan DA .2001.** How to do BPA really. *Journal of Biogeography*, 28, 345-358.
- Brooks DR, MacLennan DA. 2003.** Extending phylogenetic studies of coevolution: secondary brooks parsimony analysis, parasites, and the great apes. *Cladistics*, 19, 104-119.
- Brooks DR, MacLennan DA. 2001.** A comparison of a discovery-based and an event-based method of historical biogeography. *Journal of Biogeography*, 28, 757-767.
- Brundin L. 1966.** Transantartic relationships and their significance. *Kungliga Sweska Vetenskapsakademiens Handlingar*, 11, 1-472.
- Croizat L. 1958.** *Panbiogeography*. Published by the author, Caracas, Venezuela.
- Crisci JA. 2001.** The voice of historical biogeography. *Journal of Biogeography*, 28, 157-168.
- Dowling APG. 2002.** Testing the accuracy of TreeMap and Brooks parsimony analyses of coevolutionary patterns using artificial associations. *Cladistics*, 18, 416-435.
- Goulet H. 1974.** Classification of the North and Middle American species of the genus *Pelmatellus* Bates Coleoptera: Carabidae: Harpalini. *Quaestiones Entomologicae*, 10, 80-102.
- Haydon DT, Radtkey RR, Pianka ER. 1994.** Experimental biogeography: interactions between stochastic, historical, and ecological processes in a model archipelago. R.E. Ricklefs, Schluter D. eds. *Species diversity in ecological communities: historical and geographical perspectives* , University of Chicago Press, Chicago, USA. pp. 117-130.
- Hernandez-Baños BE, Peterson AT, Navarro-Siguenza AC, Escalante-Pliego BP. 1995.** Bird faunas of the humid montane forest of

Mesoamerica: biogeographic patterns and priorities for conservation. *Bird Conservation International*, 5, 251-277.

Liebherr J K. 1986. Cladistic analysis of North American Platynini and revision of the. *Agonum extensicolle* species group Coleoptera: Carabidae. *University of California Publications in Entomology*, 106, 1-198.

Liebherr JK. 1988. Redefinition of the *Platynus jaegeri* group and a taxonomic revision of the Mexican and Central American species Coleoptera: Carabidae: Platynini. *Transactions of the American Entomological Society*, 114, 167-214.

Liebherr JK. 1991. Revision and phylogeny of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda* and *Elliptoleus* Coleoptera: Carabidae: Platynini. *Bulletin of the American Museum of Natural History*, 202, 1-167.

Liebherr JK. 1992. Phylogeny and revision of the *Platynus degallieri* species group Coleoptera: Carabidae: Platynini. *Bulletin of the American Museum of Natural History*, 214, 1-115.

Liebherr JK. 1994a. Biogeographic patterns of montane Mexican and Central American Carabidae Coleoptera. *Canadian Entomologist*, 126, 841-860.

Liebherr JK. 1994b. Identification of the New World *Agonum*, review of the Mexican fauna, and description of *Incagonum*, new genus, from South America Coleoptera: Carabidae: Platynini. *Journal of New York Entomological Society*, 102, 1-55.

Matthew WD. 1915. Climate and evolution. *Annals of New York Academy of Science*, 24, 171-318.

Marshall CJ, Liebherr JK. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography*, 27, 2003-216.

Morrone JJ, Crisci JV. 1995. Historical Biogeography: Introduction to methods. *Annual Review in Ecology and Systematics*, 26, 373-401.

Nelson G, Platnick NI. 1981. *Systematics and biogeography: Cladistics and vicariance*. Columbia University Press, New York.

Noonan GR. 1986. Distribution of insects in the northern hemisphere: Continental drift and epicontinental seas. *Bulletin of the Entomological Society of America*, 32, 80-84.

Page RDM. 1990. Component analysis: A valiant failure? *Cladistics*, 6, 119-136.

Page RDM. 1994. Maps between trees and cladistic analysis of for obtaining historical associations among genes, organisms, and areas. *Systematic Biology*, 43, 58-77.

Ronquist F, Nylin S. 1990. Process and pattern in the evolution of species associations. *Systematic Zoology*, 39, 323-344.

Ronquist F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, 46, 195-203.

Rosen DE. 1978. Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, 27, 159-188.

Rosen DE. 1988. From fossils to earth history: applied historical biogeography. In Myers AA. eds. *Analytical Biogeography*, London and New York: Chapman and Hall, 437-481

Shpeley D. 1986. Genera of the subtribe Metallicina and classification, reconstructed phylogeny and geographical history of the species of *Euproctinus* Leng and Mutchler Coleoptera: Carabidae: Lebiini. *Quaestiones Entomologicae*, 22, 261-218.

Straneo SL, Ball GE. 1989. Synopsis of the genera and subgenera of the tribe Peleciini and revision of the Neotropical and Oriental species Coleoptera: Carabidae. *Insecta Mundi*, 3, 73-178.

Van Devender TR. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. *Packrat middens: the last 40,000 years of biotic change* ed. by J. L.

Betancourt, T. R. Van Devender and P.S. Martin, pp. 104–133. The University of Arizona Press, Tuscon, AZ.

Van Veller MGP. 2002. *A posteriori* and *a priori* methodologies for testing hypotheses of causal processes in vicariance biogeography. *Cladistics*, 18, 207-217.

Van Veller MGP. 2003. Cladistic and phylogenetic biogeography: the art and the science of discovery. *Journal of Biogeography*, 30, 319-329.

Van Veller MGP, Kornet DJ, Zandee M. 2000. Methods in vicariance biogeography: assessment of the implementations of assumptions 0, 1, and 2. *Cladistics*, 16, 319-345.

Wiley EO. 1986. Methods in vicariance biogeography. Systematics and evolution: a matter of diversity ed. by P. Hovenkamp. Utrecht University Press.

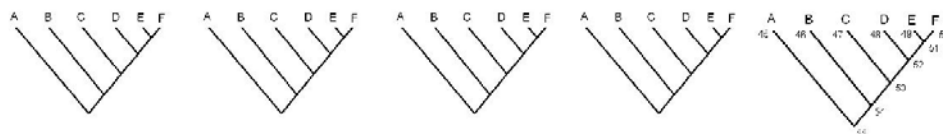
Wheeler WC. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology*, 44, 321-331.

Zandee M, Roos MC. 1987. Component-compatibility historical biogeography. *Cladistics*, 3, 305–332.

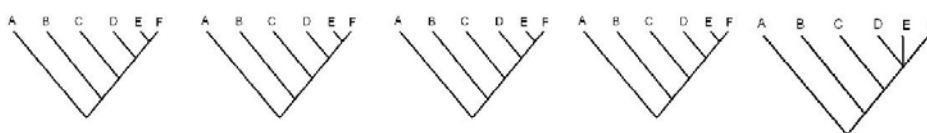
Zink RM, Blackwell-Rago RC, Ronquist F. 2000. The shifting roles of dispersal and vicariance in biogeography. *Proceedings of the Royal Society of London Series B*, 267, 497-503.

Recibido: 20 Noviembre 2005

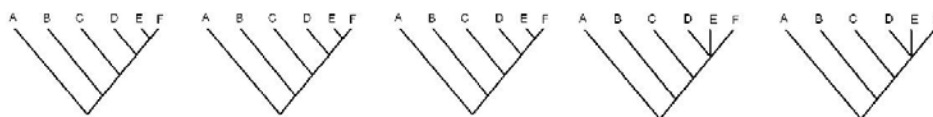
Aceptado: 16 Enero 2006

Appendix I. Theoretical scenarios used to evaluate BPA, DIVA and RTA performance.

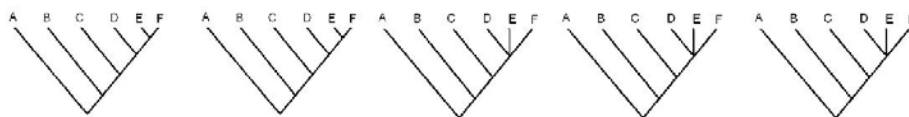
Ideal Case



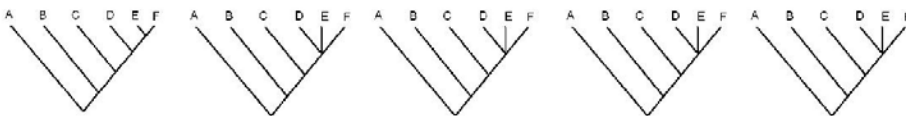
Polytomies. Pnd7-1x data set



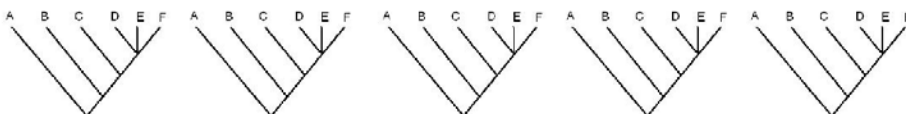
Polytomies. Pnd7-2x data set



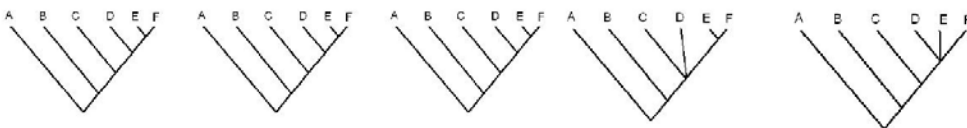
Polytomies. Pnd7-3x data set



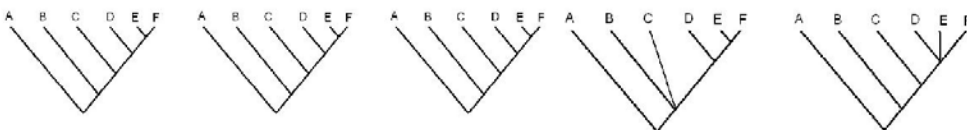
Polytomies. Pnd7-4x data set



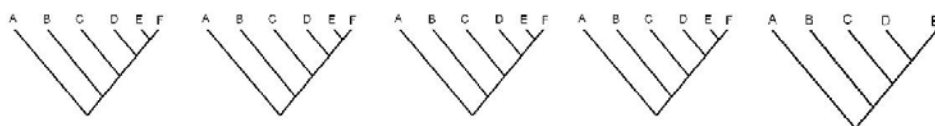
Polytomies. Pnd7-5x data set



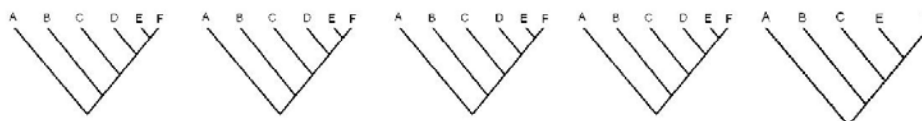
Polytomies. Pnd78-1x data set



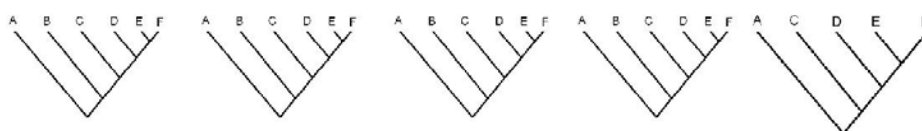
Polytomies. Pnd79-1x data set



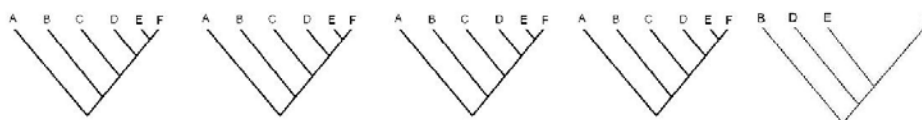
Absent areas. aa-f data set



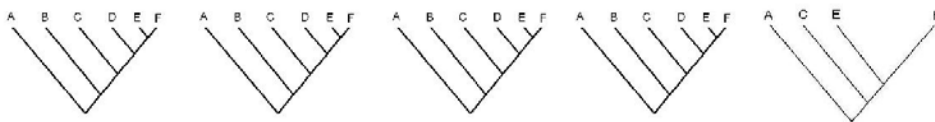
Absent areas. aa-d data set



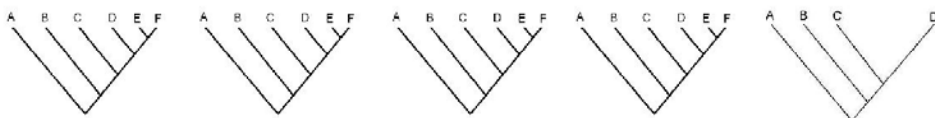
Absent areas. aa-b data set



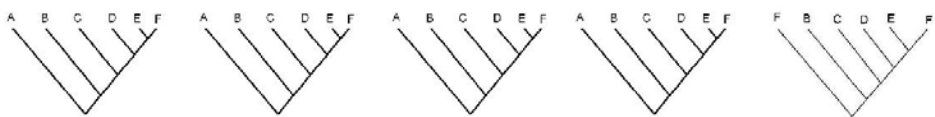
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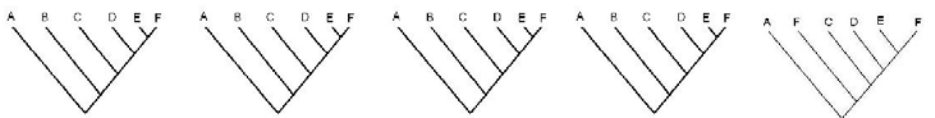
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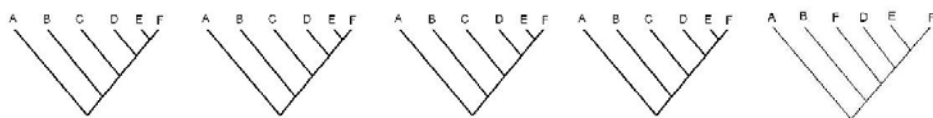
Absent areas. aa-ef data set



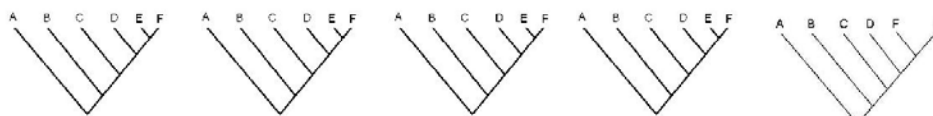
Redundant taxa. aaA-rF data set



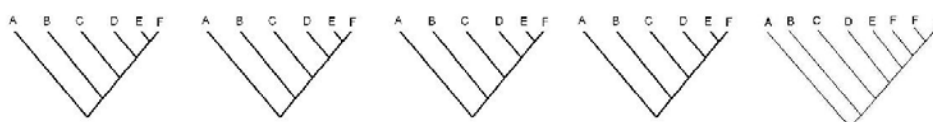
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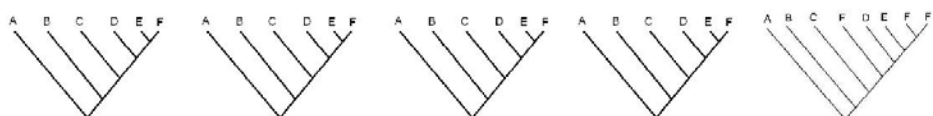
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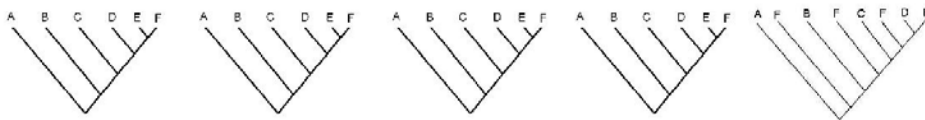
Redundant taxa. aaE-rF data set



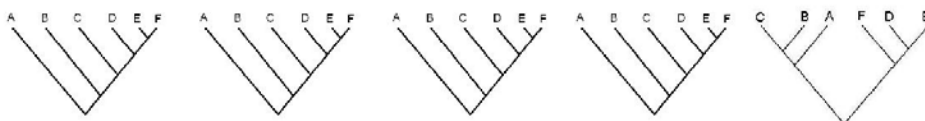
Redundant taxa. arF-a data set



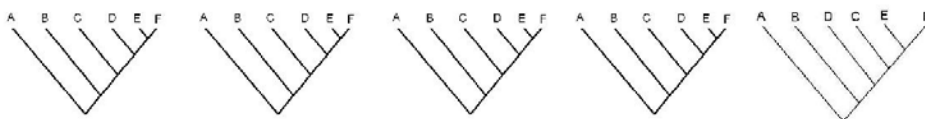
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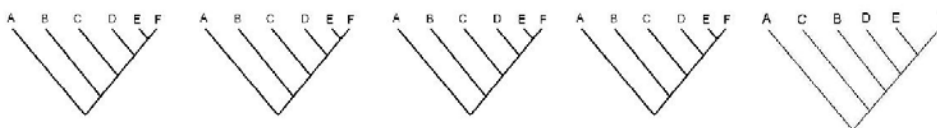
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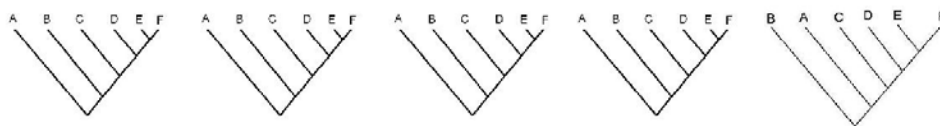
Diferent Phylogenetic relationships. dr-cld1 data set



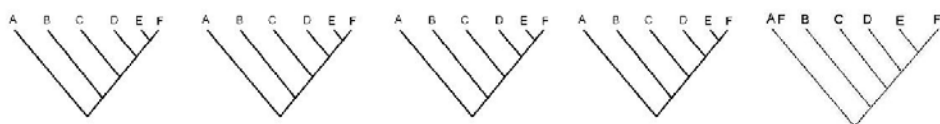
Dif. Phylogenetic relationships. dr-cld2 data set



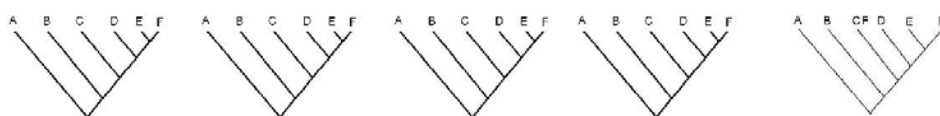
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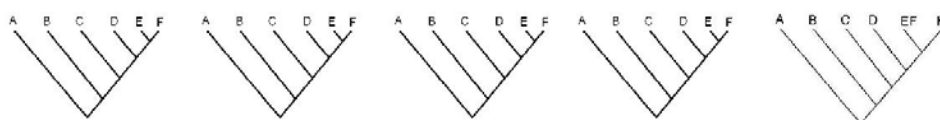
Dif. Phylogenetic relationships. dr-cld4 data set



Widespread taxa. adcl1-1x data set



Widespread taxa. adcl2-1x data set



Widespread taxa. adcl3-1x data set

