Hovenkamp’s ostracized vicariance analysis: testing new methods of historical biogeography

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Abstract

All methods currently employed in cladistic biogeography usually give contrasting results and are theoretically disputed. In two overlooked papers, Hovenkamp (1997, 2001) strongly criticized methods currently used by biogeographers and proposed two other methods. However, his criticisms have remained unanswered and his methods rarely applied. I used three different data sets to show the superiority of Hovenkamp’s methods. Both methods proposed by Hovenkamp do not suffer from the unrealistic assumptions that underlie other methods commonly used in cladistic biogeography. The method proposed in 2001 is more powerful than the previous method published in 1997, because it does not use a priori assumptions about the areas involved. However, the method proposed in 1997 may be a valid alternative for large data sets.

Historical biogeography attempts to explain geographic distributions of taxa in terms of their history rather than exclusively in terms of their current ecology. In the literature of the past 10 years, different methods for historical biogeography have been proposed, assessed and compared (Morrone and Crisci, 1995; Humphries and Parenti, 1999; Van Veller, 2000; Morrone, 2005). Thus, several authors have attempted to introduce some classification of these methods, but there is no consensus as to how these methods should be classified according to their scopes, assumptions, analytical tools, etc. (e.g., Humphries, 2000; Ebach and Morrone, 2005). Most of the confusion in the literature regarding the comparison between different methods has largely been influenced by ignoring the scope for which the methods have been developed. In fact, the scope of historical biogeography is twofold: (1) to explain current patterns of the distribution of monophyletic groups in terms of their phylogeny (taxon history), and (2) to reconstruct earth history on the basis of shared historical information recovered from phylogenies of different taxa (earth history) (Hovenkamp, 1997). For the first scope, a number of methods have been proposed, which are based on the same basic procedure: an area cladogram is constructed by substituting taxon labels for their host areas (area coding) and historical relationships between area relationships (represented by area cladograms) and taxon relationships (represented by phylogenies of the species distributed in those areas) are deduced. In the second case, different area cladograms are compared by seeking a common history for the areas involved. For the earth history scope, several cladistically founded methods have been proposed (Humphries and Parenti, 1999), but they appear theoretically problematic and empirically ineffective, without a definitive agreement emerging about procedures.

The failure of these methods to recover common patterns of earth history when applied to the same data set, probably roots in their common assumption, which appears to depart strongly from a reasonable start point, namely, area evolution is hierarchical and earth history can be contrived as a cladistic arrangement. In fact, according to Hovenkamp (1997, 2001, 2002), this is a common assumption of “cladistic biogeography”, which departs from the original aim of vicariance biogeography.

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Referring to the original definition of Rosen (1978), Hovenkamp (1997, 2001) pointed out that the target program of vicariance biogeography is to identify distribution boundaries between sister taxa in order to deduce a sequence of events that can be considered responsible for present vicariant distributions.

In his critique of current methods of “cladistic biogeography”, Hovenkamp (1997) clearly showed that: (1) evolution of areas may be reticulate; for example, assuming that “even after a collision of two land areas both areas retain their separate identities for ever after. This would be a methodological fiction rather than a realistic assumption” (p. 69); (2) as indicators of the history of areas, taxa are inherently less reliable than characters in phylogenies, because of “the much greater vagility of taxa as compared to characters” (p. 70); (3) there are scaling (area coding) problems in defining areas of endemism, because “no two taxa show exactly the same distribution” (p. 69).

In the same paper, Hovenkamp proposes a new method that, according to his proponent, should avoid these problems as it directly deals with vicariance events instead of areas. This method will be called hereafter Hovenkamp Vicariance Analysis 1 (HVA1).

Although Hovenkamp’s paper was published in Cladistics 10 years ago, his criticisms have so far gone unanswered. As it cannot be supposed that this paper was ignored, it is rather surprising that almost no author discussed the critique. In fact, Hovenkamp’s paper has been cited in subsequent papers (e.g., Humphries and Parenti, 1999, p. 66; Van Veller and Brooks, 2001; Van Veller et al., 2001b, 2003; Crisp, 2001; Crisp et al., 2001; Grandcolas et al., 2001; Hausdorf, 2002; McLennan and Brooks, 2002; Brooks and Van Veller, 2003; Siddall and Perkins, 2003), which recognized the importance of his critique, without, however, any reference to his alternative method. The only study that used HVA1 is a paper on the biogeography of four small mammals in Central Africa (Quéroil et al., 2002), where the relative ancestry based on absolute datings from mtDNA analysis is suggested as an implementation to order vicariance events from separate lineages.

However, a thorough discussion of Hovenkamp’s critique is compelling, because it implies the discarding of all methods currently used in historical biogeography, and an evaluation of HVA1 is recommended with more urgency, because there is no agreement on the correctness and utility of all currently employed methods. More recently, Hovenkamp (2001) proposed another method, hereafter called HVA2. This new method rests on the same basic procedures as HVA1, differing in the way vicariance patterns are deduced (see below). The aim of the present paper is to discuss HVA1 and HVA2 in comparison with other established methods on theoretical and empirical grounds using different data sets.

### Methods

Both HVA1 and HVA2 protocols are aimed at inferring the history of areas on the basis of a reconstruction of historical events deduced from the current distributions of taxa, allowing for both divergent (hierarchical) and reticulate patterns. The protocols are constructed so as not to be influenced by problems of area coding and do not employ taxa as characters. However, in contrast with Hovenkamp’s claims, HVA1 may be affected by problems of area coding, because areas are to be recognized and termed before the analysis is performed. By contrast, HVA2 is totally free of area coding.

Both these protocols investigate area history by identifying the location and sequence of vicariance events. Thus, earth history is resolved in terms of a sequence of vicariance events, not in terms of the relationships of areas. In the following, I summarize both methods, discussing step-by-step theoretical aspects and practical problems that might be encountered.

#### HVA1 protocol

1. For each taxon cladogram a respective area cladogram is constructed.
2. All Traceable Vicariant Events (TVEs) are enumerated. “A traceable vicariant event corresponds to a node of which both descendants occupy mutually exclusive areas. Nodes of which both descendants occupy overlapping areas are considered not traceable, and are excluded” (Hovenkamp, 1997, p. 71). According to the original protocol proposed by Hovenkamp (1997) (1) if only one TVE occurs, the cladogram is uninformative, and it should be excluded, and (2) if TVEs occur on different branches so that their relative temporal sequence cannot be specified they are uninformative and then excluded. In fact, these are unnecessary assumptions, which may prevent finding Supported Vicariance Events (SVE, see below, point 4). Therefore, the protocol should be amended to remove these assumptions, and all TVEs should be taken into account initially.

#### Practical notes

Any overlap between areas of two branches of a cladogram node disqualifies that node as a TVE. Two approaches are possible for peripatric distributions. A hard approach would be to retain as TVEs only those that can be located very precisely between nearly contiguous areas. A soft approach recognizes valid TVEs even when there is some degree of overlap between areas. As observed by Hovenkamp (1997), overlap may result from dispersal or by small-scale vicariance not resolved with the chosen size of unit areas. Because of the fractal nature of species range boundaries, what appears as an overlap at a given scale, could be resolved at a more detailed scale (higher resolution). The question is: Which degree of overlap
may be accepted as reasonably hypothesized, as spurious and due to low resolution, or due to successive dispersal? As it is impossible to have a practical, objective method, the choice will vary case by case, according to the available information on the taxa. Overlapping is a type of ambiguity, and to discover what causes ambiguity, relevant fields outside cladistic biogeography, such as ecology, ethology and physiology must be examined (e.g., Ebach, 2001). Note that a hard approach seems more conservative, but could lead to the discarding of a number of putative TVEs only by a poor resolution of a very “reasonable” dispersal after vicariance. The soft approach is less objective (it implies an evaluation of what is a “reasonable” dispersal after vicariance), but it could be more useful in finding TVEs.

3 TVEs extracted from different cladograms are compared and grouped when they specify the same vicariance events. Two TVEs can be grouped together if: (1) there is no contradiction between the two nodes in TVE, and (2) there is at least some overlap on both sides. Note that to group two TVEs, it is not necessary that the area sets on each side of the nodes are identical. Range contractions and expansions may have occurred, thus producing TVEs, which are represented by nodes whose descendants occupy areas of different extent. If range expansions after a vicariant event have determined an overlap of the two descendants, the result is overlapping areas, and thus the event cannot be recovered as a TVE. In all TVEs both descendants occupy mutually exclusive areas, but the areas may have different extents. This equals to admitting range contractions and expansions outside the area where the disjunction occurred.

4 The two compatible TVEs that have been grouped can be combined into a SVE, by combining the area sets of the TVEs. Other TVEs can then be added to the identified SVE, using the same compatibility criteria. Single TVEs (i.e., those spatially matching no other one) are discarded, because there is no reason to assume that they refer to vicariance events, instead of freak distributions (Hovenkamp, 1997, p. 71). As observed at point 2, in contrast with Hovenkamp’s (1997) assumptions, even cladograms containing only one TVE, or TVEs occurring on different branches so that their relative sequence cannot be specified, may be informative in detecting SVEs. The following example illustrates this point. Consider the following three area cladograms, where each letter specifies a hypothetical area: (1) ((X,Y) (X,Y)); (2) ((X,Y) (C(A,B))); and (3) (C(A,B)). Following Hovenkamp’s (1997) assumptions, cladogram 1 is uninformative, while in cladograms 2 and 3 the following TVEs can be recognized: A–B and C–A,B for both cladogram 2 and cladogram 3; these TVEs can be placed in two groups (say 1 for A–B, and 2 for C–A,B), which can be ordered as follows: 2 > 1. Note that the putative TVE X–Y of cladogram 1 is discarded because it occurs on different branches; as cladogram 1 is excluded, the TVE X–Y on cladogram 2 is also discarded because it is unique.

If the original protocol is amended as proposed here, the following TVEs can be recognized and retained: X–Y and X–Y for cladogram 1; X–Y, A–B, C–A,B and X–Y–C–A,B for cladogram 2 and A–B and C–A,B for cladogram 3. Now, as X–Y is supported by two cladograms, it becomes a SVE, and the following SVEs can be recognized: (1) A–B; (2) C–A,B; (3) X–Y; (4) X–Y–A,B,C. Note that, while cladogram 1 is uninformative about the position of X–Y in a sequence, the relationship of X and Y with other SVEs is stated by cladogram 2 (but if we omit cladogram 1, we cannot recognize X–Y as a SVE). Therefore, even if we cannot establish the position of X–Y (i.e., we are unable to state when X separated from Y relatively to other vicariance events), we can state the position of X,Y in respect of the other SVEs, and the following sequence can be recognized: 4 > 2 > 1.

An important assumption of the method is that a TVE, being a mere allopatric distribution of sister taxa, can actually be the result of both a true vicariance and a dispersal, because an allopatric distribution may be acquired by both events. There is no a priori reason to assume that a single allopatric pattern (identified as a TVE) is the result of a vicariance event, because vicariance and dispersal can be equiprobable. This implies that vicariance and dispersal are equally parsimonious explanations. This is, for example, in contrast to Dispersal Vicariance Analysis (DIVA) (Ronquist, 1998; see also below) which postulates a priori an extra cost for dispersal. If two or more TVEs can be grouped into the same SVE, three possible explanations can be made: (1) they can be grouped because they represent, in different taxa, the result of the same vicariance event; (2) one TVE is the product of a vicariant event, but the other is the result of a dispersal that produced the same pattern by chance; (3) both TVE are spurious, being the results of two dispersal events that produced the same pattern by chance. Explanation (1) uses one explanation (a single vicariance) to explain two patterns. Explanation (2) uses two explanations (a vicariance and a dispersal) to explain the two patterns. Explanation (3) also uses two explanations (two independent dispersals) to explain the two patterns. As explanation (1) is more parsimonious than (2) and (3), SVEs can be accepted as likely vicariance events. Note that the only theoretical assumption of this protocol is that of recurring patterns being more parsimoniously explained by a given vicariance event than by multiple dispersal. As this is also an assumption of all vicariance biogeography, it should be accepted as a reasonable start point within a parsimonious logical framework.

Practical notes. As recognized by Hovenkamp (1997), when TVEs are to be combined into SVEs, alternative
combinations of TVEs could be possible. Criteria for choosing among different combinations might be: (1) to maximize the support for a SVE, and (2) to reduce conflicting SVEs. Thus, if we have two SVEs (say A and B), each supported by two TVEs (say 1, 2 and 3, 4, respectively), but a TVE of a SVE is completely subsumed by another (say 3 is completely subsumed by 2), it is preferable to have a more supported SVE (in this case a SVE supported by 1, 2, 3, leaving off 4 as the unique pattern). If changing the SVE of a TVE reduces conflict among the succession of SVEs, this is a more parsimonious solution.

5 “On the basis of the relative ordering of cladogram nodes, SVEs can be ordered in direct pairs or series, corresponding to all the direct pairs or series extracted from the cladograms” (Hovenkamp, 1997, p. 71). To do this, each SVE can be identified by a label, and each cladogram node corresponding to a TVE included in a given SVE is replaced by the label of its respective SVE. The sequence of SVEs in a cladogram can be assessed by the sequence of the corresponding nodes. The sequences of SVEs in different cladograms are compared, and arranged in order to find a general sequence.

Practical notes. At this stage of the analysis, it may be necessary to reassess the way in which TVEs were grouped into SVEs, because there may be different ways to accomplish this, by selecting the less conflicting one(s). For example, conflicting sequences from different cladograms may be due to the fact that TVEs grouped together as supporting the same SVE actually refer to distinct vicariance events. In this case, a TVE can be grouped into another SVE or discarded.

HVA2 protocol

HVA2 rests on the same basic ideas of HVA1, but it employs a different procedure using a direct inspection of distribution maps.

1 For all nodes in the cladograms, maps are prepared showing the distributions for both descendants. For nodes including multiple terminal taxa, the distribution areas are merged.

2 Maps of nodes showing allopatric distributions are selected as indicating putative vicariance events. These maps correspond to TVEs. Maps without any clear indication of vicariance are discarded. To assess the degree with which limited overlap among peripatric distributions can be accepted, refer to point 2 of HVA1 protocol.

3 Maps supporting the same putative vicariance event are grouped together. These groups correspond to SVEs. Each group of maps is then termed as a distinct SVE. The only criterion for grouping two maps together is that the vicariance event specified by one map (represented as a track separating the two allopatric distributions) is compatible with that of the other. In other terms, the two allopatric distributions, say A and B, of a map are to be superimposed with that of a second map, say C and D, so that: (1) A and C overlap at least partially, and (2) B and D overlap at least partially, but (3) there is no overlap between A and D or between B and C. Thus, both widespread and very narrowly distributed descendants may be equally informative about the location of a vicariance event.

4 Maps showing unique patterns have to be discarded. These maps correspond to spatially unique TVEs, and thus are uninformative. However, they can be preserved for further analyses, which, with the inclusion of other cladograms, may offer the same patterns, allowing identification of other SVEs.

5 Each SVE is associated with a number of nodes in the cladograms and thus ordered into series, as at point 5 of HVA1. The final result is “one or more series of maps, with each one specifying the location of a geographic event, with the temporal order expressed by the sequence in which the maps are placed”. (Hovenkamp, 2001, p. 262).

Data sets

To assess the pros and cons of HVA1 and HVA2, I used the following three data sets, for which results obtained by other methods are also available:

1 Mesomerican poeciliid fish genera Xiphophorus and Heterandria. An earth history of Mesoamerican areas based on the phylogenies of these two taxa was initially proposed by Rosen (1978). Rosen’s data represent the classical benchmark for biogeographical analysis as almost every method and implementation has been tested with them (cf. Humphries and Parenti, 1999). Applications of Brooks’s Parsimony Analysis (BPA), Component Compatibility Analysis (CCA), Component Analysis (CA), Tree Mapping (or reconciled trees—TM) and Three-Area Statements (TAS) to this data set are discussed by Van Veller (Van Veller et al., 2000; Van Veller, 2000), while the HVA1 protocol was applied by Hovenkamp (1997) himself. The area cladograms of both taxa are reported in Fig. 1. Procedures applied to this data set are also reported in detail here.

2 De Jong’s (1998) data on tulipids, plecoptera, cholevid beetles, and newts in the western Mediterranean area. De Jong (1998) analyzed this data set using BPA, CCA, CA, TAS and the Paralogy-free Subtree Analysis (PSA). Cladograms and distribution maps may be found in the original paper. Maps constructed for HVA2 are reported in Appendix S1.

3 Phylogenies and distributions of Holarctic taxa used by Sanmartín et al. (2001). They consist of 57 cladograms, for a total of 730 nodes. All cladograms and taxon distributions can be found in the original paper, where a DIVA was applied.
Results

An analysis of Rosen’s data according to HVA1 is reported and fully discussed in Hovenkamp (1997). Use of HVA2 resulted in the identification of the vicariance events illustrated in Fig. 2. Distribution maps for unique or non-vicariant patterns are reported in Fig. 3. The vicariance events can be arranged into the single sequence 1 > 2 > 3 > 4. This sequence is the same as that obtained by HVA1.

 Regarding De Jong’s (1998) data, one cladogram did not contain any SVE and five cladograms were uninformative. HVA1 did not produce any results, because of the lack of SVEs, which can be ordered in non-conflicting direct pairs or series. By contrast HVA2 recovered some vicariance events. The informative cladograms gave 11 SVEs (Table 1). They cannot be placed into a unique linear sequence but can be arranged into a reticulate scheme (Fig. 4). These contrasting results between HVA1 and HVA2 may be explained by important differences about the treatment of areas. In HVA1, areas are coded before the analysis of vicariance events is performed. In the study case, vicariance events occurred, not between the areas as coded before the analysis, but within them. Thus, an a priori area coding that failed to recognize areas actually separated by vicariance events leads HVA1 to fail to identify SVEs.

By contrast, in HVA2, areas are defined a posteriori, after SVEs are determined. Actually, SVEs found by HVA2 cross the areas coded for HVA1, and no vicariance event was found supporting disjunctions between these areas. Looking at the results obtained by HVA2, they lead to the following ordered paleogeographic reconstruction: (1) vicariance between Iberia and Europe (event A); (2) vicariance between the Corso-Sardinia microplate and southern Europe (B), vicariance between the Iberian–Atlantic area and Europe (C), disjunction/reconnection between Iberia and North Africa (D–E), vicariance between south-west Iberia and Europe (F); (3) vicariance between Europe + Anatolia + Levant and Asia (G), followed by vicariance between north-west and south-east Anatolia (H), and vicariance between Europe and Italy south of the Alps (I); (4) vicariance between Italian peninsula and Sicily (J); and (5) vicariance between Italy and Sardinia (K).

The third data set was analyzed only by HVA1. The enormous number of taxa, and hence of nodes, prevented the possibility of making and comparing maps. Use of HVA2 should require plotting some 730 maps to be compared in searching for SVEs. It is clearly not practical, or even impossible, to trace, compare and sort into groups a large number of maps by hand. HVA1 produced a reticulate and very complex scenario. Of a total of 57 cladograms, 49 potentially useful cladograms were analyzed. A total of 13 SVEs were recognized and ordered. The historical information may be summarized in the scheme reported in Fig. 5.

Discussion

In recent years, many different cladistic biogeography methods have been proposed and heavily debated. Widely used, competing methodologies are: CA, TM, BPA and CCA. Two methods more recently formulated are TAS and DIVA. All of these methods are involved in both taxon and earth history analyses. In the earth history analysis, CA attempts to find general patterns by seeking the congruent parts of individual area cladograms; while BPA and TAS use Wagner tree parsimony to solve conflicting area relationships. BPA converts all taxon area cladograms into a combined matrix of areas and taxa, whereas TAS converts the area relationships of all nodes occurring in the taxon area cladogram into suits of three-area relationships, which are subsequently put into a matrix of areas and “statements”, represented by columns, each of which contains a three-area relationship. TM consists in reconciling taxon-area cladograms and an area cladogram that need a minimum of duplications or independent losses. All methods have their pros and cons, mostly arising from the presence of ambiguity, and its origin. The possible types of ambiguity include: wide distributions, missing areas...
and redundant (paralogous) distributions (i.e., several taxa of a given monophyletic group occurring in the same area). In CA, different assumptions (cryptically named Assumption 0, 1 and 2 and herein termed A0, A1 and A2) can be adopted to treat the incongruence encountered in constructing area cladograms and in

Fig. 2. Distribution maps and Supported Vicariance Events (SVEs) for Mesoamerican biogeography based on cladograms of Fig. 1.
comparing them. Missing areas are considered uninformative under each assumption, while they differ in the way widespread taxa and redundancy are treated. Under A0, widespread distributions are considered as the result of vicariance alone, and redundant distributions are considered valid data. CA under A0 is very similar to BPA, only differing in the treatment of missing areas: primitively absent in BPA, uninformative in CA. Under A1, widespread distributions are considered as the possible result of both vicariance and extinction, and redundant distributions are considered valid data. Under A2, widespread taxa are considered as an independent presence in every area (i.e., they can be the result of vicariance, extinction and dispersal), while each occurrence of a redundant distribution is considered separately. In BPA, missing areas can be coded as primitively absent, but absent taxa can be also treated as missing data for the relevant area (being coded as ?, and not as 0, in the matrix), while widespread taxa are treated as synapomorphies of the areas. DIVA aims at reconstructing ancestral distributions by using a three-dimensional cost matrix set up as follows: speciation event in response to vicariance costs 0, dispersal event costs 1, extinction costs 1. The best reconstruction is

Table 1
Supported Vicariant Events (SVEs) relative to the area cladograms of Mediterranean taxa reported by De Jong (1998). Nodes refer to Appendix S1

<table>
<thead>
<tr>
<th>SVEs</th>
<th>Areas of Descent 1</th>
<th>Areas of Descent 2</th>
<th>Supported by nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Iberia</td>
<td>Europe</td>
<td>42, 77, 99, 104</td>
</tr>
<tr>
<td>B</td>
<td>Corso-Sardinian Microplate</td>
<td>Southern Europe</td>
<td>73, 76</td>
</tr>
<tr>
<td>C</td>
<td>Iberian-Atlantic</td>
<td>Europe</td>
<td>53, 90</td>
</tr>
<tr>
<td>D</td>
<td>Iberia</td>
<td>North Africa</td>
<td>25, 31, 54, 97</td>
</tr>
<tr>
<td>E</td>
<td>Atlantic</td>
<td>West Mediterranean</td>
<td>23, 55, 94</td>
</tr>
<tr>
<td>F</td>
<td>South-west Iberia</td>
<td>Europe</td>
<td>44, 59</td>
</tr>
<tr>
<td>G</td>
<td>Europe, Anatolia, Levant</td>
<td>Asia</td>
<td>35, 61</td>
</tr>
<tr>
<td>H</td>
<td>North-west Anatolia</td>
<td>South-west Anatolia</td>
<td>16, 36, 103</td>
</tr>
<tr>
<td>I</td>
<td>Europe</td>
<td>Southern Italy</td>
<td>38, 46, 83, 107</td>
</tr>
<tr>
<td>J</td>
<td>Sicily</td>
<td>Italy</td>
<td>41, 84, 88a</td>
</tr>
<tr>
<td>K</td>
<td>Sardinia</td>
<td>Italy</td>
<td>15, 85</td>
</tr>
</tbody>
</table>

Fig. 3. Distribution maps for nodes showing unique or non-vicariant patterns for cladograms of Fig. 1.
that requiring the lowest total cost under a parsimony analysis. CA, CCA, TM, BPA, TAS and DIVA have been revised by a number of authors (Morrone and Carpenter, 1994; Nelson and Ladiges, 1996; Humphries and Parenti, 1999; Van Veller et al., 2000; Van Veller, 2000), under both taxon and earth history perspectives, and all show contrasting and ambiguous results. Nelson and Ladiges’s (1996, p. 54) assertion “it is doubtful [...] that the accumulated findings of cladistic biogeography of the last two decades have proven any more convincing than those of Croizat of the previous few decades” has been regarded as overly pessimistic by Humphries and Parenti (1999), but despite claims of proficiency by its proponents no method has been actually demonstrated to have a clear advantage over the others. Particularly problematic is the choice among different assumptions in CA. This problem has been strongly debated recently (Van Soest and Hajdu, 1997; Enghoff, 1998; Ebach, 1999; Van Veller et al., 1999, 2000, 2001a,b; Van Veller and Brooks, 2001), and Ebach (2001) and Ebach and Humphries (2002) pointed out that if the cause of ambiguity is not allopatry, using A0

Fig. 4. Reticulate biogeography of the Mediterranean area as inferred from cladograms and maps reported by De Jong (1998). Lettering refers to pathways reported in the Supplementary material.

Fig. 5. Reticulate biogeography of the Holarctic as inferred from cladograms reported by Sanmartín et al. (2001). Acronyms: AU, Australian Region; AF, Afrotropical Region; EN, East Nearctic; EP, East Palearctic; WN, West Nearctic; WP, West Palearctic; OR, Oriental Region. In parentheses; number of Supported Vicariance Events.
or BPA adds spurious information, leading researchers to extrapolate beyond reason. To better manage with reticulate processes, Brooks and colleagues have proposed a modified version of BPA (e.g., Brooks, 1990; Brooks et al., 2001; Brooks and McLennan, 2002). However, the effectiveness of BPA and secondary BPA has been particularly disputed (Turner et al., 2001; Siddall and Perkins, 2003; Siddall, 2004, 2005; versus Brooks et al., 2004). Even more recently, Wojcicki and Brooks (2004, 2005) proposed a new promising algorithm termed PACT (phylogenetic analysis for comparing trees). This new algorithm, which is related to secondary BPA, searches for the maximum allowable general patterns as well as unique events and reticulated relationships. However, as for BPA, the new algorithm requires a priori area coding (i.e., an a priori definition of areas of endemism) and attempts to contrive area relationships as a cladistic arrangement, although using area duplications (a questioned procedure) to represent reticulate relationships between areas (e.g., Brooks and Ferrao, 2005; Brooks and Folinsbee, 2005; Folinsbee and Brooks, 2007).

In fact, BPA (like several other methods) has been proposed to deduce information on processes that explain how taxa evolved in areas and became distributed over these areas in the scope of taxon history. Thus, the use of BPA and related methods in the earth history scope may be inherently inappropriate, although distinction between scopes has not be appreciated by most authors (including the proponents) and these methods have been subsequently applied in the earth history scope (cf. Hovenkamp, 1997). BPA and PACT strive to explain both congruent and non-congruent information with respect to taxon history, while HVA1 and HVA2 only look for congruent information in several taxon-area cladograms in order to get information on earth history. This distinction makes it difficult to compare these methods on theoretical grounds.

Rosen’s data have been profoundly tested by Van Veller (2000; Van Veller et al., 2000). Their results can be summarized as follows. An application of BPA produced four most equally parsimonious area cladograms under A0, three under A1, and 11 under A2, leading to very different alternative solutions. Solutions compatible with the sequence of vicariant events obtained by HVA1 and HVA2 may be found under each assumption. An application of CCA resulted in one cladogram under A0 and the same cladogram was found under A1; by contrast, under A2, seven new area cladograms were found, none of them present under A0 and A1. Only A2 yielded solutions compatible with the sequence of vicariant events obtained by HVA1 and HVA2. Using CA, for *Heterandria*, the same area cladogram is derived under A0, A1 and A2. For *Xiphophorus*, a single area cladogram is obtained under A0, nine area cladograms under A1, and 1165 area

cladograms under A2. Comparing the sets of area cladograms derived for both genera under A0 or A1 reveals no general area cladograms since the intersections are empty. Only under A2, are three general area cladograms found in the intersection. The resulting consensus is incompatible with the sequence of vicariant events obtained by HVA1 and HVA2. Application of TM under A0 produced a single general area cladogram. Under A1 a single, different general area cladogram was produced. Analysis of the data under A2 yields three general area cladograms, different from those obtained by A0 and A1. Only the cladogram obtained by A0 is compatible with the sequence of vicariant events obtained by HVA1 and HVA2. A TAS analysis produced a single cladogram, under both A0 and A1/A2, which is not compatible with the sequence of vicariant events obtained by HVA1 and HVA2.

Regarding De Jong’s data set, results provided by HVA2 do not fit any of the hierarchical reconstructions obtained by the methods applied by the author (De Jong, 1998). His results can be summarized as follows. Four different analyses were performed by using BPA, producing four different general area cladograms, which strongly disagree. The only recurrent clades were (Atlas and Tell Atlas) as sister to all the others, (Corsica and Sardinia) and (Iberia Palearctic Pyrenees), but the sequence of areas in the latter clades varied among cladograms. Four different analyses were performed using CCA under A0, producing four different general area cladograms, which strongly disagreed with one another and with BPA analyses. Eight different analyses were performed using CA, four under A0 and four under A1. These analyses yielded several general area cladograms, the consensus trees of which were largely polytomous and pectinate. TAS was performed under A0, yielding a single tree, and under A1, resulting in two trees; all trees were similar, but strongly contrasting with previous results. Finally, PSA was applied, using both parsimony analysis of components (resulting in three trees) and three-item statements (resulting in 30 trees). The respective consensus trees were very different, and did not fit any pattern obtained by previous analyses. As a whole, all methods used by De Jong (1998) produced contrasting results, which poorly fitted the hierarchical scenarios hypothesized on geological evidence. None of the results obtained by De Jong are compatible with HVA2 results. The results obtained by HVA2 also do not fit hierarchical scenarios, but they elucidate a reticulate pattern substantially consistent with our knowledge of the earth history of the Mediterranean basin (see Oosterbroek and Arntzen, 1992; De Jong, 1998; Blondel and Aronson, 1999; Hugot and Cosson, 2000; Palmer and Cambefort, 2000; Fattorini, 2006; for paleogeographic reconstructions). The first vicariance event (Iberia versus Europe) identified by HVA2 may be explained by the raising of the Pyreneic mountains. This
event is followed by (1) the vicariance between the Corsica–Sardinia microplate and southern Europe, which corresponds to the disjunction of the Corso–Sardinia microplate from southern Europe; (2) the vicariance between Iberian–Atlantic area and Europe; (3) the isolation of south-west Iberia (both possibly corresponding to the orogenetic processes that occurred in Central Iberia); (4) disjunction/reconnection events between Iberia and North Africa, corresponding to the continuously changing geodynamic processes of this area. After these events, two distinct patterns, each composed of different steps, may be recognized. A first pattern includes: (1) a vicariance between the Mediterranean area and Asia, and (2) a vicariance between north-west and south-east Anatolia, both interpretable as a result of glaciations, which isolated the Mediterranean area and produced climatic changes in Anatolia, leading to a disjunction of vegetation types between north-west and south-east Anatolia. A second pattern includes: (1) a vicariance between Europe and Italy south of the Alps, possibly as a consequence of glaciations on the Alps; (2) a vicariance between the Italian peninsula and Sicily (corresponding to the final disjunction of this island); (3) vicariance between Italy and Sardinia (corresponding to the final isolation of this island after the last glaciation, which, in reducing distances, may have favored some faunal exchanges).

Regarding the application of HVA1 to the Holarctic region, results may be related to paleogeographic reconstructions (cf. Humphries and Parenti, 1999; Sanmartín et al., 2001; and references therein) as follows. The first vicariance event is the disjunction of Australia from all the other regions. This vicariance may be explained by the disjunction of the Australian region from Gondwanaland. After the isolation of Australia, a disjunction of the Afrotropical region may be evidenced. After this event, two different pathways may be traced. The first pathway begins with the disjunction of the Neotropical area, referable to the breakdown of the Gondwanaland leading to the disjunction between South America and Africa. The second pathway begins with the disjunction of the Oriental region. After these events, three vicariance events can be traced: (1) a vicariance between West Palearctic + East Nearctic and West Nearctic + East Palearctic (relative to the first pathway); (2) a vicariance between West Palearctic + West Nearctic and East Palearctic + East Nearctic (relative to the second pathway, which could be the result of the breakdown of Laurasia, consisting in a disjunction of Eurasia from North America); and (3) a vicariance between West Palearctic + East Palearctic and West Nearctic + East Nearctic (from both pathways).

Finally, we found several disjunction events, supported by different numbers of SVEs. The most supported disjunction events are the intracontinental disjunctions between West Nearctic and East Nearctic (explained by the origin of the Cordillera and the effects of glaciations) and between West Palearctic and East Palearctic (explainable by the evolution of the Turgai). The well-supported vicariance between East Palearctic and West Nearctic may be referred to the disjunction of former glacial connections between these regions. Vicariance between West Palearctic and East Nearctic indicates a trans-Atlantic disjunction. Finally, trans-polar vicariance events are rare. These results are in part consistent with the results of DIVA reported by Sanmartín et al. (2001), because both methods allow for reticulate processes. However, DIVA includes dispersal events, not considered by HVA1, making it difficult to thoroughly compare the two methods.

Conclusions

When applied to the same data set, methods currently employed in cladistic biogeography give contrasting results, while also poorly fitting paleogeographic reconstructions. Resting on very different theoretical assumptions, results from HVA1 and HVA2 cannot be compared methodologically with those obtained by other techniques, but comparisons may be made about their respective results.

Results obtained by HVA1 and HVA2 may be compatible with some results of BPA, TM and DIVA, while no compatibility was found with results obtained by CA and TAS. However, this compatibility among methods may simply be the result of chance, because it has been observed for techniques that produced a large variety of alternative solutions. HVA1 and HVA2 appear to be empirically superior to all other methods not because some of their results are compatible with those produced by other methods, but because their results are in good accordance with our present knowledge of earth history.

The results obtained for the Mediterranean area and the Holarctic region are consistent with our knowledge of Earth history based on paleogeographic reconstructions. In particular, results of HVA1 and HVA2 clearly show that biotas could be strongly moulded by reticulate processes that cannot be adequately arranged into a hierarchical representation. Techniques that do not allow for reticulate reconstruction, require much compression and distortion of area relationships, and their outcome cannot be regarded as realistic representations.

Resting on similar assumptions, HVA1 and HVA2 should produce identical outcomes. This is possible only if areas are defined in the same manner in both protocols. In some circumstances (as with Rosen’s data), this actually happens. Generally, however, areas will be different. In HVA1, boundaries among areas are defined a priori, in HVA2 by a posteriori comparison of
species ranges. Moreover, HVA1 starts from taxon-area cladograms and thereby from a cladogenetic representation of relationships, a problem that affects other (cladistic) biogeographical methods. This is clearly demonstrated by the analysis of De Jong’s data set. Using HVA1 with area units, as defined by De Jong, most species showed ranges involving more than one unit, and HVA1 failed in recovering any pattern. By contrast, HVA2, proceeding directly from species ranges, avoids this problem. The negative effect of an a priori area coding is particularly dramatic when it is difficult to find natural boundaries, which can realistically suggest vicariance events. In the case of the Mediterranean area, De Jong used geographic districts as area units. HVA1 failed in recovering any vicariant pattern, because vicariance events did not occur among these districts, but through them.

No software is presently available for an automatic application of HVA1 or HVA2. For large data sets, the work required for an application of HVA2 may be very cumbersome or definitively impossible. An application of HVA1 may be more practical. If boundaries among area units may be reasonably supposed to reflect real vicariance events, HVA1 may be efficient in recovering these vicariance events (but not vicariance events within or through the areas, which can be reconstructed only by HVA2). The data set of Sanmartín et al. (2001) meets this assumption, because vicariance events certainly occurred among the continents, and HVA1 may elucidate the way they occurred.

HVA2 is more powerful than HVA1, allowing the researcher to identify vicariance events without a priori assumptions regarding the areas involved. Neither method suffers from the unrealistic assumptions that underlie other methods commonly used in cladistic biogeography. As a rule, HVA2 should be preferred, but HVA1 may be a valid alternative for large data sets.

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S. Fattorini / Cladistics 23 (2007) 1–12

11


Supplementary material

The authors have provided the following supplementary material for this article, which is available as part of the online article from: http://www.blackwellsynergy.com/doi/abs/10.1111/j.1096-0031.2007.00193.x (This link will take you to the article abstract).

Appendix S1. Distribution maps for Mediterranean taxa from De Jong (1998). Panels organization: A first section includes maps for unique or non-vicariant patterns; the second section includes Supported Vicariance Events (SVEs). Each SVE (identified by a blue line and a capital letter) is followed by maps that support it.

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