Quantitative Visualizations of Hierarchically Organized Data in a Geographic Context

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Abstract—**Here we introduce a novel quantitative technique for visualizing hierarchically organized data in a geographic context. In contrast to existing techniques, our visualization emphasizes the hierarchical relationships in the data by depicting them in a standard tree format that takes advantage of many fundamental perceptual properties. Our technique allows users to define a geographic axis and visualize how well a tree correlates with the ordering of geographical locations along this axis. This is accomplished by finding the ordering of leaf nodes, subject to the constraints of the tree topology, which minimizes the number of crossings that occur between lines that connect leaf nodes to their associated geographic locations. In this optimal layout, any crossings that occur between these lines indicate discordance between the topology of the tree and the user defined geographic axis. We have developed a branch-and-bound algorithm that allows optimal leaf orderings to be determined quickly enough to support interactive exploration of different geographic axes even for large multifurcating hierarchies. The quantitative nature of our visualization has allowed us to specify a permutation test for determining if the relationship between a tree topology and a geographic axis is statistically significant. In this paper, the utility of our visualization is demonstrated on biological data sets, but our method is applicable to any hierarchical data where geographic structure may be of interest.**

Keywords - geophylogenies; geographic visualization; tree visualization; optimal leaf ordering; crossing minimization

I. INTRODUCTION

Visualizing the hierarchical relationships within a georeferenced set of entities allows a user to explore the influence of geography on the patterns of similarity between these entities. Phylogenetic trees depict evolutionary relationships, with leaves typically corresponding to organisms or genetic sequences and internal edges showing common ancestry. While there are many published tools to visualize these trees, several recent software packages allow the binding of tree leaf nodes to the geographic locations from which the corresponding entities were sampled [1-4]. By testing the relationship between evolution and geography, these *geophylogenies* can yield valuable insights into speciation processes [5], the origin and transmission of viruses such as HIV [6] and Influenza A [3], and the long-term migration patterns of animals, including humans [7]. Additionally, by displaying underlying environmental features such as habitat type, soil acidity, or population density, spatial and non-spatial hypotheses can be contrasted or combined.

Existing geophylogenies bind leaf nodes directly to sample sites and assign meaningful locations to internal nodes by inferring their position from evidence such as dated fossils, historical samples, or biogeographic reconstruction algorithms [5]. Three-dimensional geophylogenies allow the depth of a node to be visualized as an offset from the geographic plane (Fig. 1A). This style of geophylogeny was first proposed by Kidd and Ritchie [5] and later made available as Geophylobuilder [4], an extension to ArcGIS [8]. Recently, Google Earth [9] has been used to visualize three-dimensional geophylogenies. Although Google Earth lacks the spatial analysis and environmental data integration that is possible within a GIS framework, its free availability has encouraged its use and prompted the development of a central repository for storing geophylogenies [10]. Our software package supports the same 3D representation of hierarchical data and we believe it is a powerful visualization technique when internal nodes can be assigned meaningful geographic positions.

In the absence of historical data or a plausible migration model, meaningful positions cannot be assigned to internal nodes and instead are typically placed at the spatial centroid of their children. In this case, the visualization can be misleading since it is difficult not to infer meaning from their positions. This problem persists and perhaps is even emphasized when the phylogenetic tree is viewed along the z-dimension to obtain a two-dimensional visualization (Fig. 1B). Such two-dimensional geophylogenies are also supported by the Phylogeographer [1] and the Mesquite Cartographer [2] software packages. A further weakness of these existing visualization techniques is that the relationships between entities can be obscured since the tree structure relating the entities is distorted to fit the underlying geography. In contrast, our visualization emphasizes the hierarchical relationships in the data by depicting them in a standard two-dimensional tree format where leaf nodes are visually related to their geographic locations through a series of lines which minimize visual clutter (compare Fig. 1 to Fig. 4).

Our technique can be used as an interactive exploratory tool that allows users to define a geographic axis and visualize how well the topology of the tree correlates with the ordering of geographic locations along this axis. This is accomplished by finding the ordering of leaf nodes, subject to the constraints of the tree topology, which minimizes the number of crossings that occur between lines that connect leaf nodes to their associated geographic locations. In this optimal layout, the number of crossings that occur between these lines is a
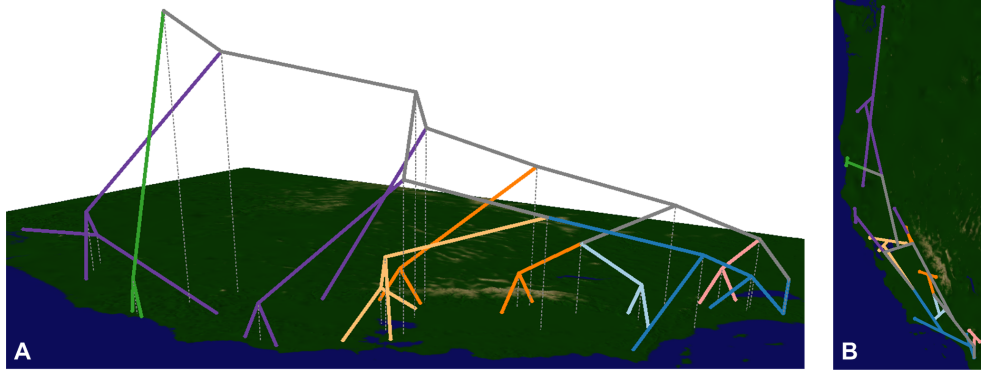
Figure 1. The visualization on the left illustrates a 3D view we have implemented in GenGIS which is typical of both Geophylobuilder and Google Earth. The same data set viewed along the z-axis is shown on the right. Visualizations such as these are possible within Geophylobuilder, Phylogeographer, and Mesquite Cartographer.

quantitative measure of the amount of discordance which exists between the topology of the tree and the user defined geographic axis. To allow interactive exploration of different geographic axes, we have developed a branch-and-bound algorithm that allows optimal leaf orderings to be determined in real time even for large multifurcating hierarchies. We support our quantitative visualization with a statistical test which determines whether the fit of tree leaves to a geographic axis is significantly better than random.

Here we demonstrate the utility of our visualization using a series of biological data sets, but our method can be applied to any hierarchical data set whose geographic structure may be of interest. Our technique has been implemented in GenGIS [11], a free and open source GIS package that provides tools for visualizing and analyzing biological data sets.

II. VISUAL DESIGN

A. Visualization overview

Our visualization consists of a number of elements (Fig. 2) the work together to allow for the rapid assessment of correlations between a tree topology and a user-defined geographic axis. Exploration of a geographic axis begins by drawing a tree layout line (TLL) to indicate the desired position and orientation of the tree. Drawing a TLL causes a geography layout line (GLL) to be generated with the geographic locations associated with the leaf nodes placed evenly along this line. The order of geographic locations along the GLL corresponds to their ordering when they are projected onto the GLL. This facilitates the rapid investigation of linear geographic axes. To explore non-linear geographic axes, an axis can be specified using a set of polylines. The order of geographic locations along the GLL will now reflect their order along this geographic axis polyline (GAP). For clarity, the start of the geographic axis and GLL are identified by a triangle.

Location lines are drawn to visually associate geographic locations with their corresponding point on the GLL. Similarly, a geographic point is visually associated with its corresponding leaf node by drawing a correlation line. As will be discussed in Section III, a critical aspect of our visualization is that the order of leaf nodes is optimized to minimize the number of crossings that occur between correlation lines.

Visual properties (e.g., colour, thickness, visibility) of all elements can be customized in order to emphasize different aspects of the data.

B. Interactive exploration of geographic axes

A number of features of our visualization support the rapid, interactive investigation of different geographic axes. Most importantly, the TLL, GLL, and GAP can be modified by dragging control points. All other elements of the visualization are automatically updated to reflect such a change. Emphasis has been placed on ensuring the visualization is updated at interactive rates (i.e., < 100 ms [12]) to ensure users can fluidly explore different geographic axes of interest.

Geographic points can either be spread evenly along the GLL or positioned in proportion to their distance from the start of a geographic axis (see Fig. 3). We support switching between these two visualization modes as they emphasize different aspects of the data. Evenly spreading out points along the GLL makes following and identifying crossings between correlation lines easier. Proportional positioning along the GLL emphasizes the distance between geographic locations along the geographic axis, and the exact ordering of locations along the GLL is more easily established.

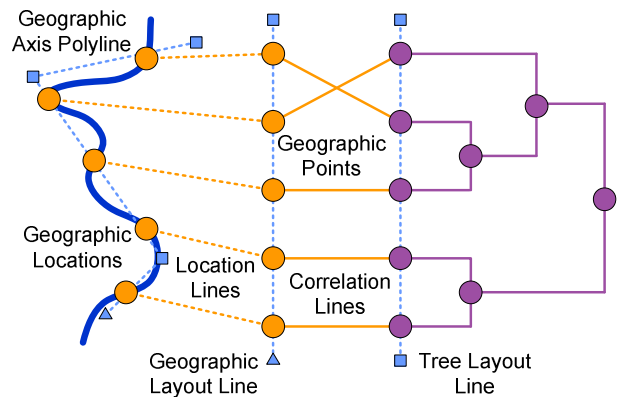To immediately determine the association between a leaf

Figure 2. Example of our visualization which relates hierarchical data depicted as a tree structure to geographic locations situated along a meandering stream. See text for details.
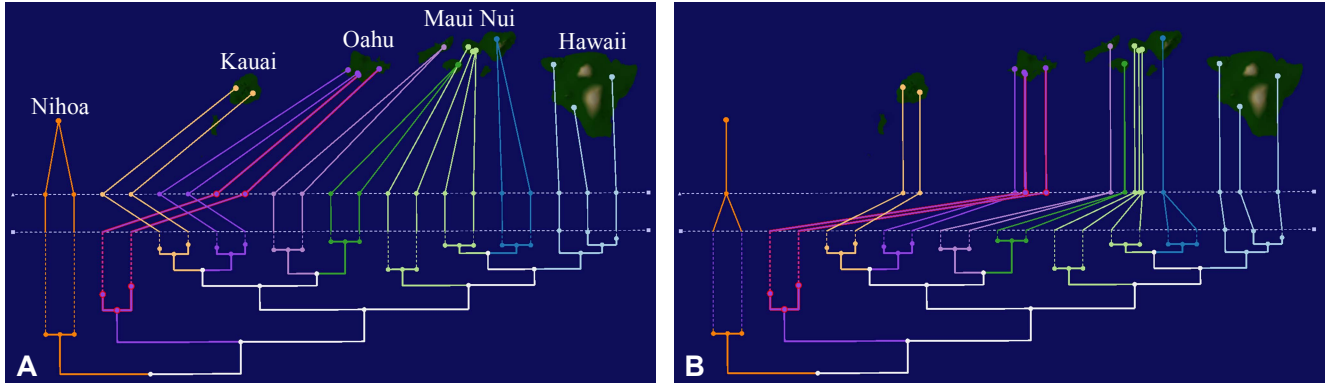
Figure 3. Visualizations of a geophylogeny for *Banza* katydids (acoustic insects) from the Hawaiian Islands. The low numbers of crossings in these images clearly indicate that there is a strong linear geographic structure underlying katydid evolution. On the left, geographic points are spread evenly along the GLL in order to emphasize crossings between correlation lines. The visualization on the right emphasizes the distance between geographic locations along the geographic axis by positioning geographic points based on their distance from the start of the geographic axis.

node, a geographic point, and a geographic location users can select any of these elements in order to highlight the others. Furthermore, internal nodes of the tree can be selected in order to highlight all elements associated with that subtree (Fig. 4). This allows users to determine if a subtree correlates strongly with a given geographic axis. For large trees, visual clutter can be reduced by drawing only those location lines that connect selected elements. This is especially useful for complicated non-linear geographic axes where location lines will necessarily cross.

Different colours can be assigned to geographic locations to emphasize important aspects of either the phylogenetic tree or the geography. These colours can be propagated up the tree in order to allow correlations to be visualized.

III. OPTIMAL LEAF ORDERING

Our visualization allows users to visually assess if a tree topology is strongly correlated with an underlying geographic axis by finding the ordering of leaf nodes that minimizes the number of crossings which occur between correlation lines. With the leaf nodes optimally ordered, the number of crossings that remain is a quantitative measure of how well the hierarchical data fits the geographic axis. In this section, we consider heuristic and approximation approaches to the NP-complete optimal leaf node ordering (OLNO) problem. These approaches are used in a branch-and-bound algorithm which allows exact solutions to be determined in interactive time for large non-binary trees.
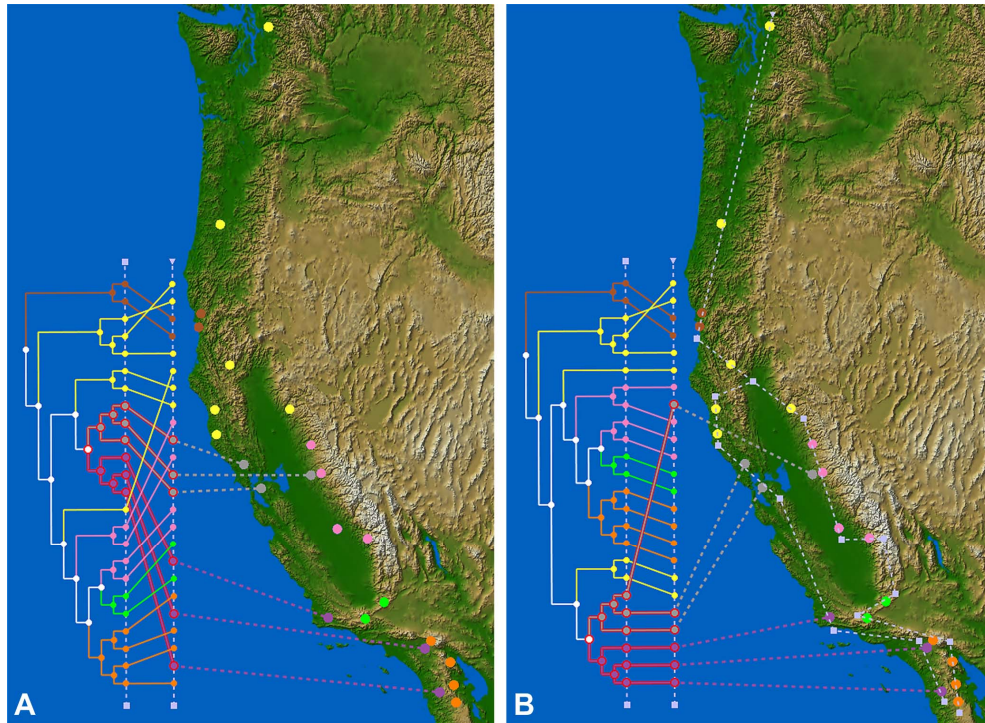

Figure 4. Visualizations of a geophylogeny for *Ensatina eschscholtzii* (salamander) from the western United States. The visualization on the left tests whether the phylogenetic tree correlates with a linear geographic axis along the coastline. This hypothesis results in 39 crossings. The visualization on the right tests whether the phylogenetic tree correlates with a non-linear geographic axis where there are two diverging paths of evolution. This hypothesis results in only 16 crossings.

A. Important theoretical results

Dwyer and Schreiber [13] have shown that determining the OLNO for a tree can be divided into a set of independent sub-problems. Specifically, they demonstrated that the optimal ordering of the children of any internal node can be found independently. For binary trees, a number of quadratic algorithms have been developed which make use of this independence property [13-15]. However, minimizing the number of crossings for a general k-ary node is equivalent to finding a solution to a common graph layout problem known as the one-sided crossing minimization (OSCM) problem.

The OSCM problem can be stated as follows: place vertices from one bipartition, V_{Fixed}, of a bipartite graph at prescribed positions along a straight line and find the position of the vertices from the other bipartition, V_{Free}, on a parallel line such that the number of straight line edge crossings will be minimized. The fixed bipartition, V_{Fixed}, is equivalent to the geographic points along the GLL and the free bipartition, V_{Free}, is equivalent to the leaf nodes on the TLL. This problem is known to be NP-complete even when all vertices of V_{Fixed} have degree 1 and all vertices of V_{Free} have degree of at most 4 [16].

Finding a solution to the OSCM problem requires an algorithm for determining the number of crossings that occur for a given ordering of vertices in V_{Free}. The most efficient algorithm known for counting edge crossings was proposed by Barth and Mutzel [17]. This algorithm runs in $O(n \log k)$, where k is the number of children of an internal node N and n is the number of leaf nodes in the subtree rooted at N.

B. Heuristic and approximation algorithms

A number of heuristic and approximation algorithms have been proposed for the OSCM problem. Heuristic and approximation algorithms can be used to determine an upper bound on the minimum number of edge crossings. This tight upper bound will allow an exact solution to the OSCM problem to be efficiently solved using a branch-and-bound algorithm.

The barycentre and median heuristics have been widely used to allow computationally efficient layouts of large graphs to be obtained [18]. A classic study by Jünger and Mutzel [19] demonstrated that the barycentre heuristic often gives results that are extremely close to the actual minimum number of crossings and generally outperforms the median heuristic (along with all other heuristics considered in the study). However, given the low computational cost of these two heuristics, it is often reasonable to employ both and use the one resulting in the fewest number of crossings.

Approximation algorithms determine solutions which are guaranteed to be within a constant factor of the true answer. By convention, approximation algorithms for the OSCM problem are given as a constant factor above a canonical lower bound, L, which is computed as follows [20]:

$$L = \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} \min(c_{ij}, c_{ji}) \qquad (1)$$

where c_{ij} is the number of crossings which occur between nodes i and j when node i is to the left of node j. The c_{ij} terms can be combined into a *crossing matrix* which indicates the number of crossings between any two nodes. The best known approximation algorithm has been designed by Nagamochi and gives a 1.4664-approximation [20].

C. Branch- and-bound algorithm

The above results suggest an *exhaustive search* algorithm can solve the OLNO problem for a complete k-ary tree in $O(h \, k! \, k^h \log k)$ time, where h is the height of the tree. This runtime can be derived by noting that a subtree for a node at height i has k^i leaf nodes. To find the OSCM for the subtree all $k!$ possible orderings must be considered. Using the Barth and Mutzel algorithm to calculate edge crossings requires $O(k! \, k^i \log k)$ work. Since there are k^{h-i} nodes at height i, the amount of work required for *each* layer of the tree is $O(k! \, k^h \log k)$.

Performing an exhaustive search is impractical in an interactive environment when $k > 5$ even for small trees and prohibitive for large trees when $k > 4$ (Fig 5). In order to allow our visualization to be applied to larger trees of higher degree, we have developed a branch-and-bound algorithm for solving the OLNO problem. Our algorithm allows interactive exploration of different geographic axes to be performed on small trees when $k \leq 8$ or large trees when $k \leq 7$.

Our branch-and-bound algorithm is given in Algorithm 1. It significantly reduces the amount of computation required to solve the OSCM problem by only considering nodes of a permutation tree that can produce a solution with fewer crossings than the currently specified upper bound. As such, it is important to seed the algorithm with a tight upper bound in order to minimize the portion of the permutation tree which must be considered. This can be efficiently done by making use of the heuristic and approximation algorithms discussed above. To solve the OLNO problem, Algorithm 1 must be applied to each internal node in the tree which can be done in parallel if multiple processors are available.
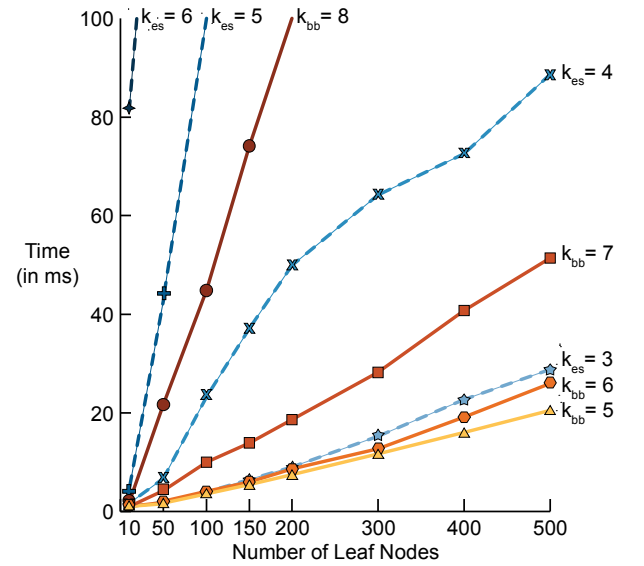

Figure 5. Running time to determine the OLNO using the branch-and-bound (solid lines) and exhaustive search (dashed lines) algorithms for various complete k-ary trees. Times are averages over 250 independent permutations of the geographic points. Experiments were performed on a single core of a 2.66GHz Intel Core 2 Quad Q9450.

```
Input: node to find optimal ordering of, upperBound on number of
crossings, crossingMatrix where crossingMatrix[i,j] = c_ij
Require: node.children is the vector of node's children, sort(vector,i)
which sorts elements of vector that are ≥ i in descending order,
next_permutation(vector) will given the next permutation of vector in
lexicographically ascending order
Return: ordering of node.children which minimizes the number of
crossings

procedure OptimalOrdering(node, upperBound, crossingMatrix)

{ a vector that indicates a permutation of the children nodes }
permutation = [0, 1, ..., node.numChildren – 1]

do
  crossings = 0

  { count number of crossings for current permutation }
  for i ∈ { x ∈ Z: 1 < x < |node.children| } do
    for j ∈ { x ∈ Z: 0 < x < i } do
      crossings = crossings + countMatrix[permutation[i],permutation[j]]
    end for

    if crossings ≥ upperBound then
      sort(permutation, i+1)
      break from for loop
    end if
  end for

  if crossings < upperBound then
    upperBound = crossings
    optimalOrder = permutation
  end if
while next_permutation(permutation) == TRUE

return optimalOrder
```

IV. Significance Test

To support our visualization, we wish to test whether or not the fit of ordered leaf nodes to geographic points along a GLL is significantly better than expected by chance alone. A Monte Carlo permutation test can be used to test this null hypothesis by holding the tree topology, geographic axis, and order of geographic points along the GLL constant while permuting how leaf nodes are assigned to geographic points. After each random permutation, the new optimal ordering of leaf nodes is determined and the number of edge crossings is determined. By generating many random permutations, an estimate of the probability density function of the number of crossings for a given tree topology and order of geographic points can be determined. The reported P-value is the fraction of permutations that have a number of crossings fewer than or equal to the number of crossings in the original model.

V. Results

Allopatry is a widely accepted method by which new species arise from populations of a single species that have become isolated due to physical barriers. Here we demonstrate how the proposed technique can be used to illustrate allopatric speciation and test different hypotheses about the geographic axis under which a population may have evolved.

A. Banza katydids: Linear geographic axis

The phylogenetic tree of *Banza* katydids from the Hawaiian Islands has recently been recovered by Shapiro et al. [21] using modern molecular techniques. This phylogeny along with its relationship to the geography of the Hawaiian Islands is given in Fig. 3. To emphasize the geographic structure, locations from each of the major geographic areas within the Hawaiian Islands (e.g., Hawaii, East Maui, Lanai) have been assigned a unique colour.

Testing a linear geographic axis along the island chain shows that the evolution of *Banza* katydids has been strongly influenced by geography. In fact, only a single subtree (highlighted in red) is not in perfect correlation with this geographic axis, which results in eight crossings occurring between the correlation lines. Applying our statistical test with 10,000 permutations indicates that the relationship between the leaf nodes and geographic locations along this geographic axis is significant at $P \leq 0.0001$.

The lack of correlation of only a single subtree with the geographic structure of the Hawaiian Islands provides valuable evidence as to the biogeographic history of the *Banza* katydids. Shapiro et al. used a manually constructed geophylogeny in conjunction with information on the geographic history of the Hawaiian Islands and inferred dates of speciation events to suggest plausible scenarios in which katydids dispersed amongst the different islands. Of particular note, Shapiro et al. take the discordance between the *Banza* phylogeny and island geography as evidence that the common ancestor of all *Banza* probably lived on Oahu.

B. Ensatina eschscholtzii: Non-linear geographic axis

The salamander *Ensatina eschscholtzii* of the western United States is a classic example of allopatric speciation [22]. Here we demonstrate how our visualization technique can be used to investigate two alternative hypotheses about the biogeographic history of these salamanders.

We first consider the hypothesis that these salamanders originated in the redwood forests of southern Oregon and migrated down the western United States during periods of greater humidity. This hypothesis is illustrated in Fig. 4A, where 39 crossings between the correlation lines occur. This is significantly non-random at $P \leq 0.0004$, which provides support for this hypothesis. However, by assigning unique colours to each sub-species we can see that this geographic axis results in many of the sub-species being highly intermixed as indicated by the heterogeneous distribution of colours along the GLL.

An alternative hypothesis is that as the salamanders moved down the western United States they dispersed down the coastal and inland ranges [23]. This hypothesis is shown in Fig. 4B and results in only 16 crossings which is significantly non-random at $P \leq 0.0001$. The colour of points along the GLL is now far more homogeneous, providing strong support for this hypothesis. Crossings that occur with this geographic axis have important biological and geographic significance. For example, the highlighted geographic point in Fig. 4B is the cause of several crossings. This point is from the Sierran population of the *xanthoptica* sub-species which is found primarily along the

coast. It is hypothesized that the Sierran population evolved from the coastal population during a mesic (moderately moist) period of the Pleistocene epoch [22].

VI. DISCUSSION

Our initial visualization did not include a GLL and instead correlation lines directly connected leaf nodes to geographic locations. This obscured the order of points along a geographic axis and resulted in crossings occurring over a large visual area which made quickly judging the number of crossings difficult. Use of the GLL resolves both of these issues by explicitly showing the order of geographic locations along a geographic axis and restricting the correlation lines to a small visual area. In addition, by spacing points evenly along the GLL, the angle between a correlation line and the GLL is a direct indication of how well the geographic location associated with that line relates to the tree topology.

Unlike existing geophylogenies, our visualization clearly depicts the hierarchical relationships in the data by presenting these relationships in standard tree formats which many researchers have experience interpreting and which take advantage of many fundamental perceptual properties [24]. However, for data sets where meaningful positions can be assigned to internal nodes three-dimensional geophylogenies may be more appropriate. For this reason, we have implemented support for both types of geophylogenies within GenGIS.

Finding the optimal ordering of leaf nodes allows our technique to be quantitatively interpreted. This quantitative property allows our visualization to be used as an exploratory tool for investigating how well alternative geographic axes correlate with a given tree topology. The interactive nature of our visualization encourages users to examine multiple hypotheses which can be evaluated based on the number of crossings they induce and the proposed statistical test. Exploration of non-linear geographic axes is supported by allowing axes to be specified by a set of polylines. This is flexible, but can be time consuming when an axis is relatively complex. We plan to extend GenGIS to allow users to specify a geographic axis by selecting one or more polylines in a shapefile (e.g., which specify a river), which will also allow the exact same geographic hypothesis to be applied to different data sets, or by different users.

Researchers are using the ever-increasing amount of available biological sequence data to explore the relationship between evolution and geography, with applications as diverse as epidemiology, speciation and microbial ecology. Our algorithm and associated statistical test will allow users to explore these relationships in a rigorous fashion, even for trees that contain many thousands of leaves.

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