

Notes and Comments

Congruence, Consensus, and the Comparative Phylogeography of Codistributed Species in California

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ABSTRACT: Comparative phylogeography has emerged as a means of understanding the spatial patterns of genetic divergence of codistributed species. However, researchers are often frustrated because of the lack of appropriate statistical tests to assess concordancy of multiple phylogeographic trees. We develop a method for testing congruence across multiple species and synthesizing the data into a regional supertree. Nine phylogeographic data sets of species with different life histories and ecologies were statistically compared using maximum agreement subtrees (MAST) and showed a high degree of concordancy. A supertree combining the different phylogeographic trees was then computed using matrix representation with parsimony, and the groups defined by this supertree were tested against climatic data to investigate a potential mechanism driving divergence. Our data suggest that species and genetic lineages in California are shaped by climatic regimes. The supertree method in combination with MAST represents a new approach to test congruence hypotheses and detect common geographic signals in comparative phylogeography.

Keywords: California, comparative phylogeography, maximum agreement subtrees, supertrees.

Whereas phylogeography seeks for the relationships between genetic divergence and geographical barriers within a species (Avice et al. 1987; Avice 1998, 2000), comparative

phylogeography assesses the congruence of phylogeographic trees for codistributed species (Avice et al. 1987; Bermingham and Moritz 1998; Avice 2000). If similar forces affected population processes across multiple species located in the same geographic region, then we would expect these species to share major similarities in the structure of their phylogeographic trees. As such, congruence among phylogeographic trees of codistributed species should be considered as indirect evidence of common geological and historical processes shaping broadscale patterns of biodiversity. Comparative phylogeography is also thought to reflect the long-term stability of the current species assemblage (Zink 2002). However, several ecological and genetic factors can cause incongruence (Cracraft and Prum 1988; Zink 1996, 2002; Templeton 1998; Avice 2000). Consequently, the power of comparative phylogeography is greatly increased when distantly related taxa with different life-history traits, demographic strategies, and ecological adaptations are used to test for common phylogeographic patterns (Zink 2002; Zamudio and Savage 2003). Moreover, measurement of congruence should not be based solely on visual comparisons of phylogeographic trees; it must be tested using statistical methods designed specifically to do so.

A serious limitation of comparative phylogeography, with respect to phylogenetics, is that the trees considered often represent different species with nonidentical geographic distributions. Therefore, phylogeographic trees that use specific localities as operational taxonomic units (OTUs) cannot be directly compared. Unless some regional units or geographical boundaries are defined a priori as the OTUs (i.e., leaves of each tree), it is difficult to combine the trees with one another (the same limitations apply to vicariance biogeography; van Veller et al. 2003). A related problem stems from the fact that these geographical regions are usually defined from the results of previous analyses that detected genetic breaks concordant with biogeographic boundaries. Therefore, the regional units are not independent from the data, which probably explains why so many studies are based on visual

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comparisons of different trees rather than statistical evaluation (e.g., Kelemen and Moritz 1999; Ditchfield 2000; Riddle et al. 2000; Weisrock and Janzen 2000; Arbogast and Kenagy 2001; Zink et al. 2001; Pastorini et al. 2003; Parker et al. 2004).

For the same reason, phylogeographic trees have not been combined using consensus methods. This is explained by the independence of the leaf sets under comparison, but it also relates to the fact that phylogeographic trees are not always defined on the same regional units. In the rare cases where they are, supertree methods (Sanderson et al. 1998; Bininda-Emonds et al. 2002; Bininda-Emonds 2004a) can be used to amalgamate trees (see Hall and Harvey 2002). Specifically, this approach amounts to combining phylogeographic trees of different species exhibiting partially overlapping (sympatric) distributions. A combination of independent trees not only increases density of geographical coverage, it also can be used to detect common signals across several species. The resulting phylogeographic supertree, defined on the total area represented by the combination of the different source trees, can also be used to detect geographical breaks in the data. The corresponding regions can then be statistically tested against independent data, for example, by assessing whether climatic variables are significantly correlated with the breaks defined by the supertree. This information can be used to test hypotheses regarding the proposed mechanisms generating divergence and speciation across a geographic region.

The existence of multiple phylogeographic data sets of species with broad distributions across the state of California (for a summary, see Calsbeek et al. 2003) provides a case to illustrate the application of supertrees in comparative phylogeography. California has a unique biological diversity and leads North America in terms of numbers of native and endemic species (Ricketts et al. 1999; Myers et al. 2000; Stein et al. 2000). The California Floristic Province is also one of the 34 world hot spots of biological diversity (Myers et al. 2000; Mittermeier et al. 2005). This bioregion has a history of complex plate tectonic activity, volcanism, ocean inundation, and mountain uplift that has resulted in a diversity of habitats with distinct geographic boundaries. Sharp elevation gradients cause abrupt ecotonal regions that differ in climatic regimes and hence may be selective agents on species. Consequently, if the multiple source trees are congruent, we hypothesize that the phylogeographic regions defined using a supertree approach will be statistically different with respect to climatic variables. Incongruence among source trees would lead, however, to a supertree without any phylogeographic signal and in turn with no relationship to climatic factors.

Several methods are currently available to conduct statistical analyses and evaluate a priori hypotheses in com-

parative phylogeography and historical biogeography (Taberlet et al. 1998; Edwards and Beerli 2000; Sullivan et al. 2000), including tests of isolation-by-distance measuring the correlation between genetic and geographical distances (e.g., Turner et al. 1996; Calsbeek et al. 2003). Specifically, Brooks parsimony analysis (BPA; Brooks 1985; Brooks et al. 2001) has been used to combine different area cladograms in a single tree (Taberlet et al. 1998). Tree reconciliation methods (Page 1994) also have been used to test for congruent geographic patterns of independent gene trees using randomization tests (Sullivan et al. 2000). In a different context, Edwards and Beerli (2000) used a coalescent model to develop a likelihood ratio test of diversification of multiple species pairs.

Here we propose a new way to compare several source trees representing overlapping geographical regions using maximum agreement subtrees. We then show how to assemble the trees using a supertree approach to obtain a synthetic estimate of genetic divergence for all species. Although matrix representation with parsimony (MRP) has been used in a biogeographic framework to assemble trees obtained from morphological characters (Hall and Harvey 2002), this study represents the first application of supertrees in a comparative phylogeographic context using trees generated from DNA sequence data.

Material and Methods

For the purpose of this project, nine phylogeographic studies representing widely different taxonomic groups were selected in order to detect common patterns among co-distributed species. The data sets represent mitochondrial or nuclear DNA sequences of three amphibian, two mammal, one reptile, one bird, one insect, and one plant species, with numbers of individuals ranging from 15 to 127 and with partially sympatric distributions in California (table 1). These data sets were selected because the taxa are widely distributed throughout the state of California, and we were interested in the phylogeographic history of the entire bioregion. In addition, we were able to obtain the original sequence data and alignments directly from the authors. In order to compare and further combine the phylogeographic trees representing different taxa with overlapping geographical ranges, the original data were recoded to define common regional units. These regional units could have been defined in a variety of ways. For example, a grid of regularly spaced hexagons could have been used; however, in our case, many of those cells would not contain any data. Alternatively, the 10 Jepson bioregions of California (Hickman 1993), used in the California GAP analysis, may have been selected to recode the data; however, in that case, we would not be authorized to test the resulting supertree against climatic variables because

Table 1: Source data sets used to compute congruence tests and build a supertree of California

Scientific name	Common name	Genes (bp)	No. individuals	No. counties	Source
<i>Aneides lugubris</i>	Arboreal salamander	ND4 and Cytb (2,727)	46	16	L. J. Rissler, unpublished manuscript
<i>Batrachoseps</i>	Slender salamanders	Cytb (784)	127	31	Jockusch and Wake 2002
<i>Lampropeltis zonata</i>	Mountain king snake	ND4 (787)	25	20	Rodriguez-Robles et al. 1999
<i>Lessingia</i>	Lessingia (plant)	18S-26S nuclear rDNA and ITS + ETS (1,203)	38	22	Markos and Baldwin 2001
<i>Neotoma fuscipes</i>	Dusky-footed woodrat	Control region and Cytb (1,284)	15	12	Matocq 2002
<i>Sorex ornatus</i>	Ornate shrew	Cytb (801)	25	10	Maldonado et al. 2001
<i>Timema</i>	Walking stick	COI (416)	48	10	Law and Crespi 2002
<i>Taricha torosa</i>	California newt	Cytb (778)	49	19	Kuchta 2003
<i>Baeolophus</i>	Titmouse	Cytb (300)	30	13	Cicero 1996

these same variables are used, in part, to define the bioregions. Instead, we chose a county-based approach to recode the phylogeographic trees using common regional units. Counties represent geographical as well as political units and can thus facilitate interpretation of our results in conservation and management contexts (see Dobson et al. 1997, 2001; Seabloom et al. 2002). Therefore, each individual specimen in a given study was recoded as the county from which it was sampled. Matrices of corrected distances among pairwise sequences were then computed using a K2P model (Kimura 1980) to treat all data in a coherent fashion (other models provided almost identical results). Finally, average distances between counties were calculated from the corrected distances, and these average matrices were submitted to a neighbor-joining (Saitou and Nei 1987) algorithm in PAUP* (Swofford 2002) to build the county trees corresponding to the different data sets (the same trees were obtained with a least-squares algorithm). These nine trees were used to perform congruence analyses and construct a supertree of California counties.

Congruence was assessed through maximum agreement subtrees, computed in PAUP*, for all pairwise combinations of county trees. A maximum agreement subtree (MAST) is the largest possible tree compatible with a given pair of source trees (Finden and Gordon 1985). Therefore, this approach is appropriate to compare trees bearing different numbers of leaves representing partially overlapping or inclusive regions, as is the case here. The size of a MAST can be used as a congruence index; the larger the MAST, the more congruent are the trees compared. When trees of different sizes are compared, a normalized congruence index must be defined, however. It is computed as the size of a MAST divided by the number of leaves in common for the trees compared. A normalized MAST score of one indicates that the pair of trees is topologically identical when restricted to the same set of leaves (i.e., counties). It is worth noting that the congruence of trees with only

three counties in common will always have a score of one, since there exists only one possible unrooted tree topology with three leaves.

The significance of a normalized MAST score can be determined with a randomization test. For a given pair of trees, the test consists of generating pairs of random trees with the same number of leaves as the original trees and computing, in turn, their score. The trees are declared congruent when the normalized MAST score is greater than expected by chance alone. In other words, the test is significant when the original score is greater than or equal to the vast majority of scores (e.g., 95% for $\alpha = 0.05$) computed from pairs of random trees of the same sizes as the original trees. When more than two trees are compared at the same time, the average of the normalized MAST scores computed over all pairwise comparisons of trees (i.e., 36 pairs in this case) is used to test the null hypothesis that the input trees are not more congruent than a set of random trees with the same number of leaves. Practically, the significance of this test is assessed with randomization by generating 1,000 sets of random trees of the same size as the nine original trees, using a uniform distribution in PAUP*. The average of the normalized MAST scores among those trees is then calculated to construct a distribution of the test statistic under the null hypothesis. When the actual trees are shown to be more congruent than expected by chance alone, they can be combined with a supertree approach.

Several different techniques have been proposed to compute supertrees, depending on what properties are desired and the types of trees being combined (Bininda-Emonds 2004b, and references therein). Among these alternative approaches, MRP is the more common method of supertree construction in phylogenetics (Baum 1992; Ragan 1992), but only once has MRP been applied to biogeography (see Racheli 2004). The standard MRP method relies on a binary matrix representation of each tree using ad-

ditive coding. The elements of that “pseudocharacter” matrix for all trees (nine in the present case) are combined in a single matrix, and the leaves (i.e., counties) that are not in a given tree are coded as missing in the corresponding matrix element. The combined matrix is then analyzed with parsimony to compute one or more most parsimonious MRP supertrees. The supertree of California counties was constructed using RadCon (Thorley and Page 2000) to generate the pseudocharacter matrix and PAUP* to compute the MRP supertree.

In order to test whether the groups that could be defined on the supertree are significantly different with respect to climatic regimes, MANOVA was computed in STATISTICA using 10 different variables: relative humidity (coefficient of variation of monthly values, maximum across all months), precipitation (total annual precipitation, coefficient of variation of monthly precipitation, precipitation in the driest quarter of the year), radiation (coefficient of variation of monthly values, maximum across all months), and temperature (coefficient of variation of monthly values, mean diurnal range across months, maximum across all months). The chosen variables were those used in multiple ongoing studies in the Museum of Vertebrate Zoology at the University of California at Berkeley (L. J. Rissler, R. J. Hijmans, C. H. Graham, C. Moritz, and D. Wake, unpublished manuscript). The climate data are summarized means of data from Daymet (<http://daymet.ntsg.umd.edu/default.html>), covering 18 years of temperature, radiation, precipitation, and humidity at a 1-km² scale. We used ArcView 3.2 to compute these means on a county basis. In addition to the MANOVA, a distance-based multiple regression analysis (Legendre et al. 1994) was also computed using the program Permute! (available from <http://www.bio.umontreal.ca/Casgrain/en/labo/permute/>). To do so, the branch distance matrix corresponding to the MRP supertree was used as the dependent variable, and Euclidean distance matrices computed from the 10 climatic descriptors were used as independent variables. Backward and forward selection procedures were employed to select the significant variables, and regression models were tested with 999 permutations.

Results

The nine county trees obtained from the different data sets are presented in figure 1. The size (number of counties) of those trees ranges from 10 to 31, for a total of 46 counties represented overall. Not a single county was included in all trees, and the maximum number of counties in common between any two trees was 12. Table 2 provides information about the overlap between pairs of trees and the corresponding size of MAST scores. The multiple comparison test assessing the congruence among all nine

county trees is highly significant (average normalized MAST score = 0.71, $P < .001$; table 2) and indicates that the different taxa share a significant phylogeographic signal. A combination of all trees is thus warranted to compute a supertree of the 46 counties of California.

The MRP supertree combining the nine trees in figure 1 is presented in figure 2*b* (a color version of fig. 2 is available in the online edition of the *American Naturalist*). It depicts the relationships among the 46 counties of California included in at least one of the input trees. That supertree was then used to define geographic breaks and test whether the corresponding groups made sense in terms of climatic variables. There exists many ways to cut a tree so as to define groups characterized by subtrees (e.g., using bootstrap values, Bremer support, or branch lengths). One such possible classification of counties into five arbitrary groups is presented in figure 2*c* to illustrate the testing procedure.

Precipitation (annual precipitation and precipitation during the driest quarter of the year), radiation (coefficient of variation of monthly radiation), and temperature (coefficient of variation of monthly temperature) were significantly different between the five groups defined by the supertree (Wilks's $\lambda = 0.022$, $F = 5.32$, $df = 10, 40$, $P = .000$). In other words, similarities and differences in the climatic regime among counties closely correspond to the subtrees defined by arbitrary cuts of the supertree. Furthermore, the same variables were selected by the multiple regression model of the branch distance matrix of the MRP supertree against the climatic descriptors ($R^2 = 0.34837$, $P = .001$). Clearly, there is a common signal in the underlying phylogeographic structure of the combined county trees representing nine different taxa. In addition, our results suggest that these differences are significantly shaped by climate.

Discussion

Numerous studies exist on the phylogeography of codistributed species in California, but these studies do not explicitly examine the congruence in phylogeographic patterns among the species (Calsbeek et al. 2003, and references therein). Even when we take radically different species with different life histories and ecologies, the overall picture in California is one of concordancy, and our analyses revealed the strength of that congruence. Furthermore, the groups defined by the supertree were shown to be significantly related to differences in climatic variables. Interestingly, these groups also correspond closely to different bioregions, and a supertree constructed using such bioregions proved to be very similar to the county-based supertree (results not shown). This suggests that natural selection and/or vicariant events may have operated at

Table 2: Pairwise comparison of phylogeographic trees for the computations of maximum agreement subtrees (MAST) scores

	a	b	c	d	e	f	g	h	i
a. <i>Aneides lugubris</i>	...	7	5	5	4	5	4	6	3
b. <i>Batrachoseps</i>	13	...	7	10	6	7	5	7	6
c. <i>Lampropeltis zonata</i>	6	16	...	7	3	5	5	7	5
d. <i>Lessingia</i>	9	18	12	...	5	5	4	5	5
e. <i>Neotoma fuscipes</i>	4	10	3	6	...	4	3	5	5
f. <i>Sorex ornatus</i>	5	10	9	6	4	...	4	4	5
g. <i>Timema</i>	5	8	7	6	3	5	...	4	5
h. <i>Taricha torosa</i>	10	14	9	8	7	6	6	...	4
i. <i>Baeolophus</i>	3	9	5	7	7	5	5	7	...

Note: The values in the lower triangle are the number of counties in common between two trees, and the values in the upper triangle are the size of the maximum agreement subtrees for the two trees compared. The normalized MAST score is computed as the ratio of these two values. The average normalized MAST score for all 36 pairwise comparisons is 0.71, which is highly significant ($P < .001$).

small spatial scales in California (<25 km²) and not only at the larger scale of bioregions. In fact, recent work using bioclimatic modeling in California (L. J. Rissler, R. J. Hijmans, C. H. Graham, C. Moritz, and D. Wake, unpublished manuscript) also shows tight environmental envelopes of species. Each taxon provides some unique and often complementary information. For example, *Baeolophus* unites the distant Inyo and Lassen counties (fig. 1i). Relatively little additional information is present in the avian phylogenetic tree, perhaps as expected due to extensive polytomies in the phylogeny of bird species studied in California (Zink 1991; Barrowclough et al. 1999; Zink et al. 2000). The supertree also shows linkages between coastal and Sierran counties. This transvalley leak is evident from phylogeographic trees in multiple species (e.g., *Aneides lugubris* and *Taricha torosa*) where individuals from the Bay region are most closely related to individuals in the Sierra Nevada (fig. 1a, 1h). Molecular divergence dates across multiple taxa also coincide with putative data for uplift of the Sierra Nevada, Coast, and Transverse mountain ranges (Chamberlain and Poage 2000; Calsbeek et al. 2003). Therefore, natural selection across abrupt climatic zones and vicariant events caused by geologic activity produced a strong genetic congruence in phylogeographic patterns and high endemism.

The power of comparative phylogeography resides in the detection of common signals that could not have been recognized using a single phylogeographic tree (Bermingham and Moritz 1998; Arbogast and Kenagy 2001). However, concordance in the biogeographical patterns of codistributed species requires adequate statistical tests that account for the fact that the trees compared represent different species with overlapping distributions in only parts of their range. Phylogeographic congruence can be measured using the statistical methods developed in phy-

logenetics to compare trees, but these tests assume that the trees are defined on common regions. We have used maximum agreement subtrees to assess and test the congruence of phylogeographic trees. MASTs have well-known statistical and algorithmic properties (Gupta and Nishimura 1998) and are also used in phylogenetics to compare trees (Swofford 1991). For comparisons of only two trees, reconciled trees maximizing the number of covariance events (Page 1994; Page and Charleston 1998) can also be constructed to assess the significance of shared history between the taxa. Similarly, BPA can be applied to detect common patterns among overlapping trees (Brooks et al. 2001). However, the assumptions of these methods are not always respected with phylogeographic trees, and statistical tests are not readily available to account for dispersal, extinction, or vicariance events (Van Welzen et al. 2003).

Despite the recent popularity of supertree methods to construct large phylogenies (e.g., Bininda-Emonds et al. 1999; Liu et al. 2001; Jones et al. 2002; Kennedy and Page 2002), the properties of these approaches are not fully understood yet (Wilkinson et al. 2005). For one, MRP supertrees differ from other methods that rely on matrix representation with distances (MRD), such as the average consensus procedure (Lapointe and Cucumel 1997). In the present application, topological relationships alone were accounted for in building the supertree, but a totally different pattern could have been obtained with alternative methods that account for branch lengths. When branch lengths are set to one, as is the case here, MRP and MRD supertrees should provide similar results (Lapointe et al. 2003). What prevented us from using actual branch lengths was the large fraction of missing cells in the combined matrix because of the poor overlap among the county trees. More importantly, the same problem also precluded the use of any statistical evaluation of phylogenetic errors, such

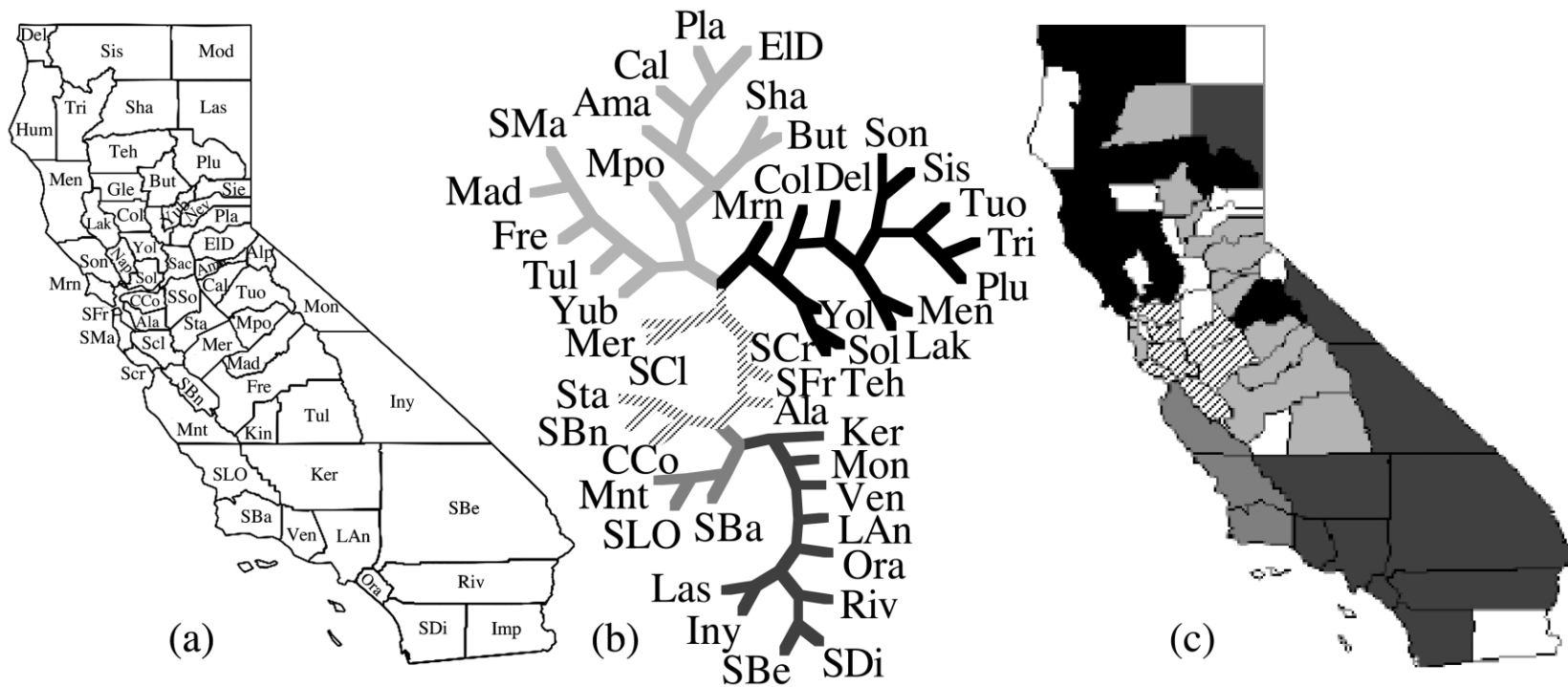


Figure 2: *a*, Map of California showing the location and abbreviations for the counties used in this study. *b*, Matrix representation with parsimony supertree computed from the nine trees in figure 1, with the corresponding groups defined by the different subtrees mapped onto the counties of California. *c*, The counties in white were not represented in any of the input trees. *Ala* = Alameda, *Ama* = Amador, *But* = Butte, *Cal* = Calaveras, *Col* = Colusa, *CCo* = Contra Costa, *Del* = Del Norte, *EID* = El Dorado, *Fre* = Fresno, *Iny* = Inyo, *Ker* = Kern, *Lak* = Lake, *Las* = Lassen, *LAN* = Los Angeles, *Mad* = Madera, *Mrn* = Marin, *Mpo* = Mariposa, *Men* = Mendocino, *Mer* = Merced, *Mon* = Mono, *Mnt* = Monterey, *Ora* = Orange, *Pla* = Placer, *Plu* = Plumas, *Riv* = Riverside, *SBn* = San Benito, *SBe* = San Bernardino, *SDi* = San Diego, *SFr* = San Francisco, *SLO* = San Luis Obispo, *SMA* = San Mateo, *SBa* = Santa Barbara, *SCL* = Santa Clara, *SCr* = Santa Cruz, *Sha* = Shasta, *Sis* = Siskiyou, *Sol* = Solano, *Son* = Sonoma, *Sta* = Stanislaus, *Teh* = Tehama, *Tri* = Trinity, *Tul* = Tulare, *Tuo* = Tuolumne, *Ven* = Ventura, *Yol* = Yolo, *Yub* = Yuba. A color version of figure 2 is available in the online edition of the *American Naturalist*.

as the bootstrap or the jackknife. It is clear that the reliability of supertrees must be assessed through resampling and randomization procedures, and specific methods have been developed to do so (see Lapointe and Cucumel 2003). Still, supertrees are not phylogenies, and their validation and interpretation is somewhat different. Specifically, the incompatibilities in the data do not have to be interpreted as homoplasy but rather depict different signals in the data with respect to topological relationships in the multiple source trees (Bininda-Emonds 2004a). When used properly, supertrees represent powerful tools to test congruence hypotheses and detect common geographic signals across multiple trees of codistributed species. Nevertheless, further studies are badly needed to evaluate the relative performance of competing approaches, using either simulations or real data. In the meantime, our use of methods for assessing congruence and building supertrees across multiple phylogeographic trees provides a novel, integrative, and powerful approach to comparative phylogeography.

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