

Clustering of Contact Zones, Hybrid Zones, and Phylogeographic Breaks in North America

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ABSTRACT: A recent test for the existence of suture zones in North America, based on hybrid zones studied since 1970, found support for only two of the 13 suture zones identified by Remington in 1968 (Swenson and Howard 2004). One limitation of that recent study was the relatively small number of hybrid zones available for mapping. In this study, we search for evidence of clustering of contact zones between closely related taxa using data not only from hybrid zones but from species range maps of trees, birds, and mammals and from the position of phylogeographic breaks within species. Digital geographic range maps and a geographic information system approach allowed for accurate and rapid mapping of distributional data. Areas of contact between closely related species and phylogeographic breaks within species clustered into areas characterized by common physiographic features or predicted by previously hypothesized glacial refugia. The results underscore the general importance of geographic barriers to dispersal (mountain chains) and climate change (periods of cooling alternating with periods of warming, which lead to the contraction and expansion of species ranges) in species evolution.

Keywords: geographic information system, range boundaries, refugia, speciation, suture zones, vicariance biogeography.

There has been a resurgence of interest in suture zones in recent years as studies have indicated that hybrid zones and major phylogeographic breaks within species cluster in particular geographic locations (Hewitt 1996; Hewitt

1999; Avise 2000; Guillaume et al. 2000; Hewitt 2000; Hewitt 2001; Brunner et al. 2002; Kropf et al. 2002; Redenbach and Taylor 2002; Hewitt 2004). Hypotheses for why hybrid zones cluster in specific geographic locations were first proposed by Anderson (1948, 1949, 1953), who argued that hybrid zones, especially plant hybrid zones, would tend to cluster in areas that had recently experienced anthropogenic disturbance, a process he called “hybridization of the habitat.” In addition, he noted that hybrid zones would tend to cluster in areas between glacial refugia (Anderson 1949).

Two decades later, interest in hybrid-zone clustering was rekindled by Remington (1968), who named these clusters “suture zones” and identified 13 areas in North America where he believed these clusters occurred. Remington (1968) emphasized three explanations for the formation of suture zones. First, in common with Anderson, he noted that biotic range expansion out of shared glacial refugia could lead to the formation of suture zones at geographic midpoints between the refugia. He proposed that this type of suture zone occurs in eastern Texas and northern Florida (Remington 1968; Avise 2000). Second, Remington concluded that suture zones would form at the foothills of mountains as the result of dispersal through mountain passes during periods of climate warming. The junction of the eastern Rocky Mountain foothills and the Great Plains was given as a possible example of this type of suture zone. Finally, Remington, again in common with Anderson (1948), speculated that many suture zones could be attributed to anthropogenic changes in the landscape of North America over the course of the past few hundred years. He argued that a major suture zone south of the Great Lakes formed as the result of forest clearing activities of humans, and he further noted that it was possible that the suture zone at the junction of the eastern Rocky Mountain foothills and the Great Plains formed because human-induced changes to the Great Plains allowed eastern North American species to move across the Great Plains and meet their western relatives at the foot of the Rockies.

Additional explanations for the formation and location of suture zones have been developed by Hewitt (1996,

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1999, 2000, 2001), who observed that some of Remington's suture zones, such as the zone south of the Great Lakes and the zone in southern British Columbia, are located at the maximum extent of Pleistocene ice sheets. Typically, such zones represent meeting grounds for taxa with northern and southern forms, and Hewitt (1996, 1999, 2000, 2001) postulated that the formation of such suture zones may be attributed to rapid range expansion of northern species living at the southern edge of Pleistocene glaciers. By rapidly filling in the space opened by the retreat of glaciers, these northern species block the range expansion of closely related species living further south, a process referred to hereafter as the leading-edge hypothesis. Hewitt (1996, 1999) also appreciated the strong barriers to dispersal represented by mountain chains and noted that low mountain passes would provide corridors for dispersal during periods of climatic warming; hence, hybrid zones should cluster in such corridors. Hewitt's contention that hybrid zones should cluster in corridors within mountain chains contrasts with Remington's emphasis on foothills-plains junctions as areas of hybrid zone clustering.

Although suture zones have achieved a certain respectability among evolutionary biologists, a recent quantitative test for the existence of the 13 suture zones proposed by Remington (1968) provided support for only two (Swenson and Howard 2004): the Great Lakes (suture zone 1 of Remington) and the Rocky Mountain–Great Plains junction (suture zone 4 of Remington). This analysis also identified clusters of hybrid zones outside of Remington's original suture zones. Although the results of Swenson and Howard (2004) cast doubt on the existence of many of the suture zones identified by Remington, the authors hypothesized that the lack of support could be due to the number of hybrid zones ($n = 117$) used in the test. One solution to this issue is to await the study and mapping of many more hybrid zones in North America. Another is to expand the definition of suture zones from a cluster of hybrid zones to a cluster of contact zones, hybrid zones, and phylogeographic breaks. In so doing, phylogeographic breaks within species and areas of contact between closely related species that do not hybridize can be included in the analyses, thereby greatly expanding the number of adjoining range boundaries that can be mapped and assessed for clustering. The rationale for considering these three types of contact zones as equivalent is that the same processes that bring two distinct but hybridizing taxa together, such as postglacial range expansion from separate refugia, will bring together closely related species that are completely reproductively isolated as well as populations that have diverged so little that they are considered conspecific.

The greatest obstacle to a clustering analysis of contact zones has been the size and format of geographic range map data sets. Thousands of geographic range maps have

been available in field guides for decades but only recently have some of these data become digitally available from government and private organizations in formats that can be downloaded onto a personal computer hard drive. Once downloaded, digital geographic range maps can be imported into a geographic information system (GIS), which allows fast and efficient visualization and analysis of range boundaries. However, there is a major drawback to using these large digital data sets; namely, the data are typically digitized by hand from paper maps, which can introduce errors in the representation of range size, boundaries, and shape (Gaston 2003; Qian and Ricklefs 2004). Thus, the selection of which data sets to use is crucial. Errors in broadscale digital data can be minimized by empirical checks performed by the institution creating the digital maps. Fortunately, there are North American data sets available, such as the U.S. Geological Survey Tree database and the NatureServe avian and mammalian databases, that implement these types of checks and thereby make it possible to conduct broadscale contact zone analyses.

This study analyzes clustering of contact zones in order to address several major questions. Specifically, (1) Where do contact zones cluster in North America? (2) Are there physiographic similarities among areas of clustering? (3) Is clustering consistent with previously hypothesized glacial refugia and postglacial expansion routes in North America? (4) Do contact zone clusters occur in the same locations as the suture zones identified by Remington in 1968? In the "Discussion," we also examine similarities in the means by which North American and European suture zones are formed.

Methods

Digital Geographic Range Maps

Geographic range maps of 292 North American tree species were downloaded from the U.S. Geological Survey (<http://climchange.cr.usgs.gov/data/atlas/little>). These maps are digital representations of geographic range maps compiled by Little and his colleagues in the United States Department of Agriculture (Critchfield and Little 1966; Little 1971, 1976, 1977).

Avian geographic range maps were downloaded from the NatureServe website (<http://www.natureserve.org>). These data were provided by NatureServe in collaboration with Robert Ridgely, James Zook, the Nature Conservancy Migratory Bird Program, Conservation International Center for Applied Biodiversity Science (CABS), World Wildlife Fund US, and Environment Canada WILDSPACE (Ridgely et al. 2003). The NatureServe Western Hemisphere avian range data set currently contains information for 4,336 species. A total of 241 of these avian species were

utilized in this study. We limited our data set to those species with ranges wholly contained within North America that form a contact zone with a congeneric species also occurring only in North America.

Mammalian range maps were also downloaded from the NatureServe Web site. These data were compiled by NatureServe in collaboration with Bruce Patterson, Wes Sechrest, Marcelo Tognelli, Gerardo Ceballos, the Nature Conservancy Migratory Bird Program, Conservation International Center for Applied Biodiversity Science (CABS), World Wildlife Fund US, and Environment Canada WILDSPACE (Patterson et al. 2003). The NatureServe Western Hemisphere mammalian range data set currently contains information on 1,712 species; again, we limited our attention to North American species, of which 363 formed contact zones with a congener.

Contact Zone Mapping

We initially imported all 6,340 digital geographic range maps from the three separate data sets into the geographic information system (GIS) ArcView 9.0 (Environmental Systems Research Institute 2003). Inside the GIS we placed all the range map layers representing a particular genus onto a map of the Western Hemisphere using an Alber's Equal Area Projection. As noted above, species ranges that were not limited to North America or did not overlap with a congeneric species were removed from the data set. Contact zones were generated by using the GeoSpatial Analyst extension to overlay all congeneric species exhibiting range contact or overlap. After the contact zones were generated, the remaining portions of the ranges were discarded. Whether or not hybridization occurs between two species that form a contact zone was not determined.

Hybrid Zone Mapping

Hybrid zones were mapped as described in Swenson and Howard (2004). Briefly, a literature search spanning the years 1970–2002, using seven article databases, was conducted for terrestrial North American hybrid zones. The four truncated keywords used for this search were “cline,” “contact zone,” “hybrid zone,” and “hybridization.” The locations of populations from hybrid zones identified through this literature search were plotted within the GIS as zero-dimensional points. Hybrid zones containing three or more reported populations were converted into two-dimensional polygons using a minimum convex polygon technique, which creates polygons with no internal angles greater than 180°. This technique was used because of its independence from frequency distributions when creating polygons from distributions of points. Other point-to-polygon techniques, such as a harmonic mean and an

adaptive kernel, rely on frequency distributions, causing them to enlarge areas with greater point densities.

Hybrid zones containing only two reported populations were converted into polygons within the GIS using a two-step approach. First, a linear map layer was created by connecting the two point populations with a straight line. Second, a 5-km buffer was placed around this straight line to create an area representing the hybrid zone. Hybrid zones containing one reported population were converted into polygons within the GIS using a one-step approach. A buffer was placed around the population to give a circular area with a radius of 5 km. A 5-km buffer was used for both two- and one-population hybrid zones because a buffer of this size provides the most conservative hybrid zone area that can still be detected by the GIS. This buffering approach reduces the amount of commission error (overextrapolation of hybrid zone area) and therefore reduces unsubstantiated hybrid zone overlap.

Phylogeographic Break Mapping

A literature search was performed for the truncated keywords “phylogeography” or “phylogeographic break” in the ISI Web of Knowledge article database. This literature search was performed in February 2005. All phylogeographic breaks that were located outside of North America or were aquatic were excluded from our analysis. Each phylogeographic break was plotted in the GIS first as a set of points and then converted to a two-dimensional area as described above for the hybrid zone mapping process.

Taxon-Specific, Hybrid Zone, and Phylogeographic Break Spatial Clustering Analysis

Each vector map layer of adjoining range boundaries, hybrid zones, and phylogeographic breaks was converted into a raster map layer within the GIS at a resolution of a half degree. The raster layers for each individual taxonomic group (for example, mammals) were overlaid within the GIS to give a new map layer that had a value for each grid cell representing the number of contact zones, hybrid zones, or phylogeographic breaks occurring at that specific location. This process resulted in five map layers (trees, birds, mammals, hybrid zones, and phylogeographic breaks) that were each analyzed separately. Initially, a Getis-Ord general G statistic that measures whether high grid cell values cluster anywhere in North America was calculated within the GIS (Getis and Ord 1992; Ord and Getis 1995). For all five groups, these calculations gave a significant result. We then utilized a Getis-Ord local G statistic to detect the precise locations of hot spots of clustering (Getis and Ord 1992; Ord and Getis 1995). A hot spot is defined as a geographic area where there is a sta-

tistically significant level of clustering of multiple hybrid zones, phylogeographic breaks, and/or contact zones.

Combined Spatial Clustering Analysis

We combined the five raster map layers from each of the five groups by overlaying them within the GIS. The resulting map had a value for each grid cell that gave the number of contact zones, hybrid zones, and phylogeographic breaks occurring at that location. This map layer was subjected to the same global and local Getis-Ord analyses described above (Getis and Ord 1992; Ord and Getis 1995).

Analysis of Remington's Suture Zones

A contingency table χ^2 analysis was performed to test whether the amount of spatial overlap between contact zone hot spots identified from the combined analysis and Remington's (1968) suture zones was greater than expected by chance. Briefly, any given location in North America was placed into one of four categories: (1) within both a suture zone and a hot spot; (2) within a hot spot only; (3) within a suture zone only; or (4) outside all suture zones and all hot spots. The expected values of the four categories were obtained by (1) multiplying the observed percent hot spot area by the observed percent suture zone area; (2) multiplying the observed percent hot spot area by the observed percent no-suture zone area; (3) multiplying the observed percent no-hot spot area by the observed percent suture zone area; and (4) multiplying the observed percent no-hot spot area by the observed percent no-suture zone area. A similar approach was used to evaluate whether any particular suture zone showed a stronger association with hot spots than expected by chance alone. Significance of these individual tests was evaluated in two ways, without correcting for multiplicity and by utilizing the sequential Bonferroni adjustment (Holm 1979).

Analyses of Refugial Locations

Following Endler (1982) we analyzed the distribution of contact zone positions between hypothesized refugia (fig. 1). We began by identifying eight hypothesized refugia from the literature (Daubenmire 1975; Rogers et al. 1991; Liston et al. 1992; Parks et al. 1994; Osentoski and Lamb 1995; Walker et al. 1995; Sewell et al. 1996; Soltis et al. 1997; Comes and Kadereit 1998; Roman et al. 1999; Walker and Avise 1998; Austin et al. 2002; Kropf et al. 2002; Austin et al. 2004). These refugia were chosen for examination because their geographic positions are well defined and because they have been broadly discussed in the North American phylogeographic literature and in recent suture

zone literature. We tested for midpoint clustering by drawing migration routes (described in the phylogeographic literature) linking refugia and then plotting the number of contact zones along lines representing these routes. If the histograms resulting from these analyses are unimodal and peak near the geographic midpoint between hypothesized refugia, then the existence of these refugia and the expansion routes are supported. A unimodal histogram that is skewed toward one refugium or the other also provides support for the refugia if the skewing is associated with barriers to dispersal. If the histogram does not exhibit unimodality or is bimodal, peaking in or near the hypothesized refugia, then the refugia are not supported (Endler 1982). Because hybrid zone, phylogeographic break, and contact zone "richness" did not exhibit patchiness on a fine scale, minor deviations in expansion routes or refugial locations would not affect the results. Thus, these histogram analyses should be considered only coarsely sensitive to the location of the hypothesized refugia and to the location of postglacial expansion routes.

Results

Adjoining Range Boundaries

The 292-tree species range maps pointed to the existence of 1,135 adjoining range boundaries between congeneric species within North America (see app. A in the online edition of the *American Naturalist*). The genus containing the most contact zones was *Quercus* ($n = 535$). The genus *Pinus* gave rise to the second-largest collection of contact zones ($n = 331$). The 241 avian species ranges yielded 249 contact zones. The genus containing the largest number of contact zones was *Toxostoma* ($n = 17$; app. A). We identified 879 mammalian contact zones from the 363 species range maps studied. The genus *Peromyscus* contained the largest number of mammalian contact zones ($n = 184$) followed by *Tamias* ($n = 88$) and *Sorex* ($n = 80$; app. A).

Hybrid Zones and Phylogeographic Breaks

The hybrid zone literature search identified 117 hybrid zones reporting one or more populations that could be mapped into the GIS (Swenson and Howard 2004). The phylogeographic break literature search yielded 68 different breaks that could be accurately mapped in the GIS. The literature used to map the phylogeographic breaks is available in appendix B in the online edition of the *American Naturalist*. All phylogeographic breaks that were identified in the second literature search were cross-checked against the hybrid zone literature search in order to ensure no contact zone was mapped twice.

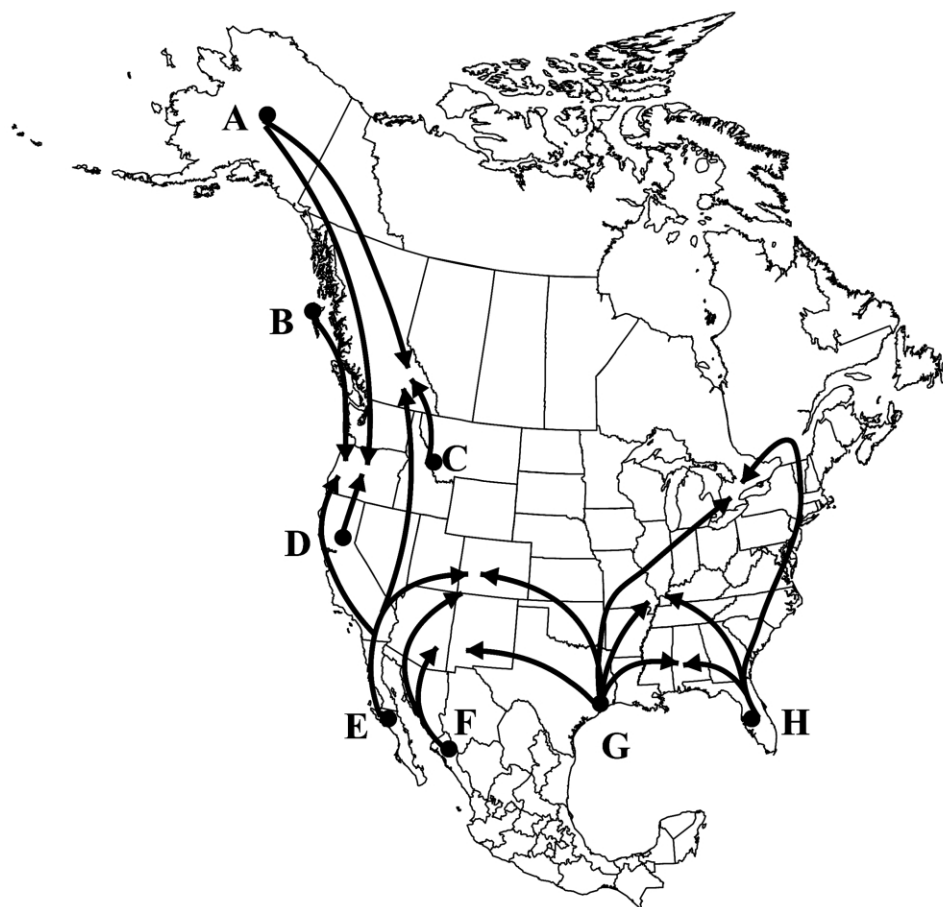


Figure 1: Hypothesized refugia and postglacial expansion routes considered in the analyses. The black circles represent hypothesized refugia, which are lettered for reference. Black arrows signify postglacial expansion routes.

Contact Zone Clustering Analyses

The global Getis-Ord G statistic yielded a significant result for tree ($Z_g = 1,497.34$; $P < .0001$), avian ($Z_g = 872.58$; $P < .0001$), and mammalian ($Z_g = 1,274.84$; $P < .0001$) range boundaries. The global Getis-Ord G statistic analysis also produced a significant result for the hybrid zone raster map layer ($Z_g = 29.40$; $P < .0001$) and the phylogeographic break map layer ($Z_g = 33.45$; $P < .0001$). Thus, all five types of contact zones mapped in this study provided global evidence of clustering.

Local Getis-Ord G statistics identified where these hot spots of clustering occurred (grid cells with $Z_{g_i} \geq 1.96$; $P \leq .05$). The grid cells with significant Z_{g_i} values were selected and mapped as a new vector map layer. Tree contact zone clustering occurred in multiple areas of North America (fig. 2a). Five large hot spots were located (1) in the Rocky Mountains north and south of the border between the United States and Canada; (2) in southern

Oregon and northern California; (3) in central and southeastern Alabama; (4) along the southern Illinois–northern Kentucky border; and (5) near the border of Sinaloa and Sonora in Mexico (along the Sierra Madre Occidental). Avian contact zones clustered primarily in western North America (fig. 2b), with large hot spots in (1) north-central Texas; (2) the east face of the Rocky Mountains; (3) southeastern British Columbia; and (4) east and west of the southeastern Arizona–southwestern New Mexico border. Mammalian contact zones also clustered primarily in the western portion of North America (fig. 2c) with hot spots in seven locations: (1) central Oregon; (2) central Sierra Nevada Mountains; (3) southern California; (4) the Rocky Mountains of northern Colorado; (5) western New Mexico; (6) western Chihuahua; and (7) eastern Durango. Hybrid zone clusters occurred across the United States (fig. 2e). The largest clusters were located (1) in the Cascade Range; (2) in the Sierra Nevada Mountains and western

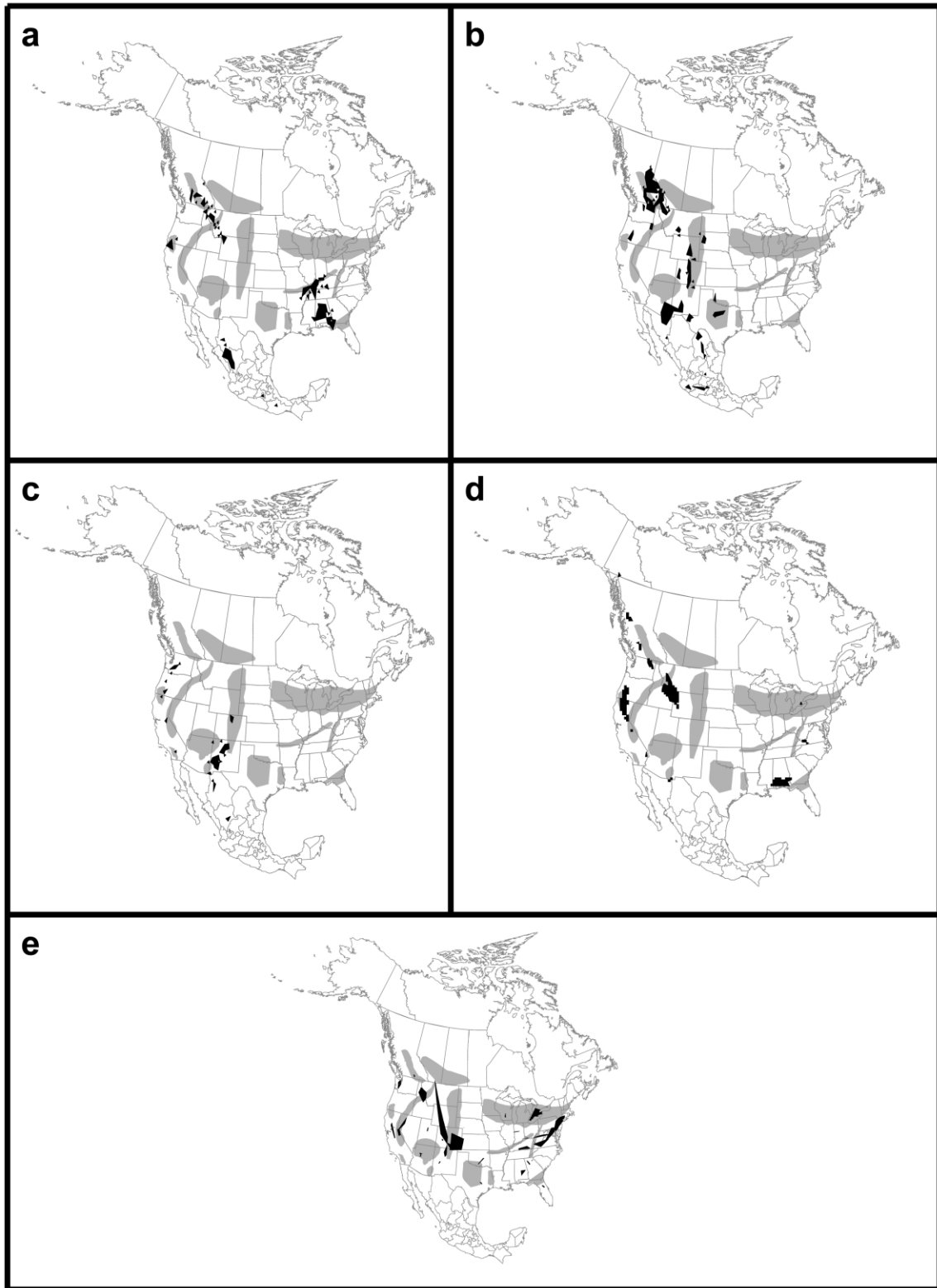


Figure 2: Hot spots of contact zone clustering in North America (*black*) and Remington's suture zones (*gray*). *a*, Tree contact zone hot spots; *b*, avian contact zone hot spots; *c*, mammalian contact zone hot spots; *d*, phylogeographic break hot spots; *e*, hybrid zone hot spots.

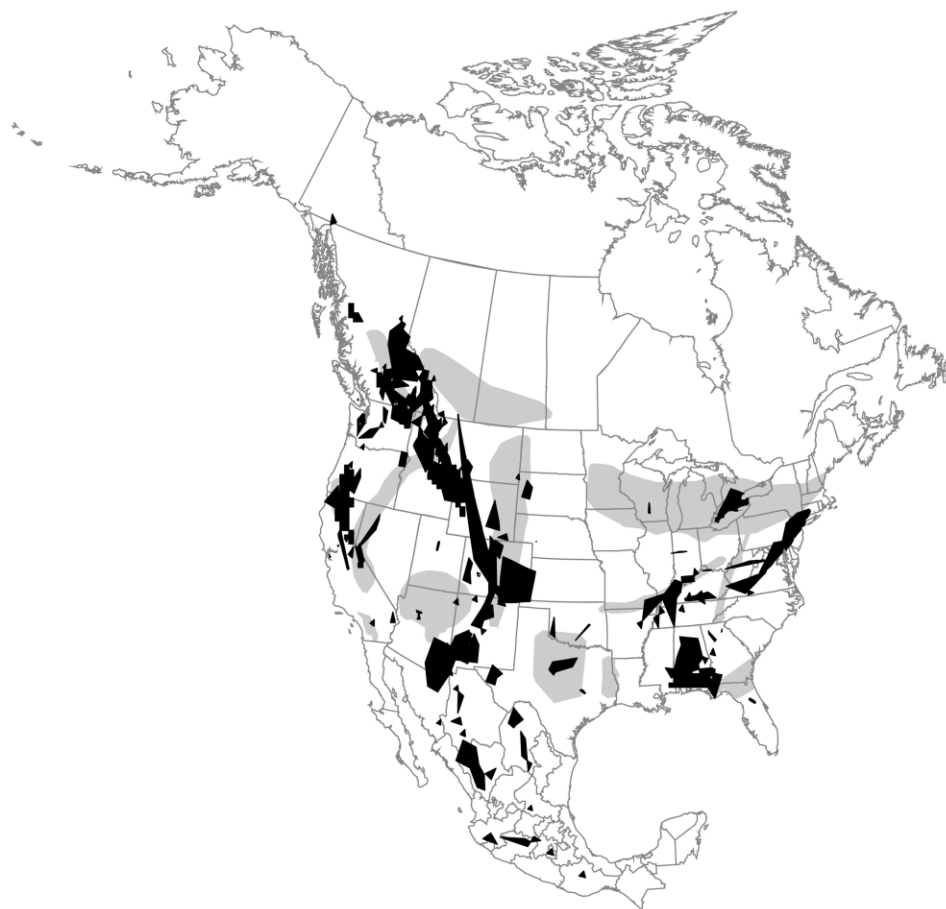


Figure 3: A map of the hot spot clusters (*black*) identified when all hybrid zones, phylogeographic breaks, and contact zones were lumped together. The gray indicates Remington's (1968) proposed suture zones.

Nevada; (3) in the Rocky Mountains of Idaho, Wyoming, Colorado, and New Mexico; (4) in eastern Colorado; (5) in the Great Lakes region; and (6) in the Appalachian Mountains. These locations are discussed in more detail in Swenson and Howard (2004). Major hot spots of phylogeographic break clustering were found in many of the same locations as contact zone clusters (fig. 2*d*). In particular, large clusters were located (1) in northern California and southern Oregon; (2) in British Columbia; (3) in the southeastern United States; (4) in Idaho, Montana, and Wyoming; (5) in southern West Virginia; and (6) in southern Ontario.

Combined Spatial Clustering Analysis and Remington's Suture Zones

As expected, given the results described above for the five individual map layers, combining map layers yielded a significant result with regard to clustering ($Z_g =$

1,195.33; $P < .0001$), and the hot spots identified with the local Getis-Ord G statistic were a compilation of the hot spots distinguished within the individual map layers (fig. 3). A digitized version of Remington's 1968 suture zone map is shown in figures 2 and 3 to allow a visual comparison with each hot spot map. Considering all contact zones together, the amount of spatial overlap with Remington's suture zones is greater than expected by chance ($\chi^2 = 6.56$; $P < .05$). Moreover, six of Remington's 13 suture zones were supported when analyzed separately ($\chi^2 > 4.5$; $P < .05$): the Great Lakes (suture zone 1), Great Plains (suture zone 4), British Columbia (suture zone A), northern California–southern Oregon (suture zone B), southeastern Arizona–southwestern New Mexico (suture zone E), and southern Illinois (suture zone G). Using a sequential Bonferroni correction, which provides a very conservative estimate of statistical significance, three of Remington's suture zones were supported: British Columbia (suture zone A), northern California–southern Oregon

(suture zone B), and southeastern Arizona–southwestern New Mexico (suture zone E).

Refugial Locations

Midpoint clustering tests (Endler 1982) provided results that support seven hypothesized refugia: A, B, D, E, F, G, and H (see fig. 1). This testing also supported 11 hypothesized pairwise postglacial expansion routes: A and E (two routes); B and D; B and E; G and H (three routes); E and G; F and G (two routes); and A and D (fig. 4). The existence of hypothesized refugia C (Daubenmire 1975; Soltis et al. 1997) and the migration route between A and C were not supported by the analyses.

Discussion

Hybrid zones, adjoining borders between closely related species, and phylogeographic breaks clearly congregate in certain areas of North America. Some of these hot spot locations are associated with obvious present-day physiographic features, while others seem to reflect expansion out of Pleistocene glacial refugia. The physiographic features most strongly associated with hot spot locations are chains of mountains. Hot spots occur in most of the major mountain chains of North America (fig. 3), including the Rocky Mountains of New Mexico, Colorado, Wyoming, Montana, Idaho, and southeastern British Columbia; the Sierra Nevada Mountains of California and Nevada; the Cascade Range of Washington, Oregon, and southwestern British Columbia; the Peloncillo Mountains of southeastern Arizona and southwestern New Mexico; the Appalachian Mountains of West Virginia, Virginia, Pennsylvania, New York, and Connecticut; and the Sierra Madre Occidental and Sierra Madre Oriental Mountains of Mexico. Hot spots are not as evident in the mountains of eastern Canada.

It is not surprising that contact zones between closely related species cluster in the mountain chains of North America. These chains typically run in a north-south direction over long distances, serving as formidable barriers to gene flow between populations on different sides, especially during periods of glaciation, the most recent of which ended about 10,000 years ago in North America (Webb and Bartlein 1992). With warming and the retreat of glaciers, eastern and western taxa can begin to move through the mountains, particularly along low elevation passes, which will serve as conduits for collisions between formerly isolated groups (Hewitt 1996, 1999). Indeed, this result mirrors the clustering of hybrid zones found by Hewitt (1996, 1999) in some of Europe's major mountain ranges (i.e., Pyrenees, Alps).

Some hot spots, even some of which are found near or

within mountain chains, can be explained, at least in part, as the result of migration from glacial refugia. In the western United States, examples of such hot spots occur in south-central Oregon and in Washington–southern British Columbia. Here, many contact zones are not between a taxon with an eastern distribution and one with a western distribution but between northerly distributed and southerly distributed taxa. Such a pattern, especially between taxa that occur west of the Cascade Range in Oregon, strongly indicates the influence of glacial refugia. California could have harbored southern populations during periods of glaciation (fig. 1; Liston et al. 1992) and northern refugia could have occurred in central Alaska, the Queen Charlotte Islands, and northern Idaho (Daubenmire 1975; Elliot-Fisk 1988; Rogers et al. 1991; Soltis et al. 1997; Comes and Kadereit 1998). Indeed, the contact zone distributional analyses presented here support the existence of all of these refugia except for the northern Idaho refuge (refuge C in fig. 1). Thus, our results suggest that closely related populations confined to northern and southern refugia diverged as a result of isolation. With the retreat of the glaciers, individuals from the northern refugia in the Queen Charlotte Islands and Alaska could migrate southward along the coast or through the ice-free corridor and individuals from the southern refugia in California and Baja California could migrate northward, eventually meeting and forming contact zones (fig. 1).

Alternatively, migration from southern refugia alone could give rise to a clustering of north-south contact zones. According to the leading-edge hypothesis developed by Hewitt (1996, 2000), northern taxa, which occur in refugia closest to the glacial maximum, rapidly expand in range following the retreat of the ice and obstruct the advance of taxa from the south, which leads to a clustering of contact zones near the glacial maximum. As noted by Soltis et al. (1997), it can be difficult to distinguish between the two scenarios outlined above, even with phylogenetic data, and it is likely that both contribute to the formation of north-south contact zones in the Pacific Northwest. Nevertheless, the presence of contact zone hot spots north of the maximum extent of the Laurentide Ice Sheet argues for the existence of northern refugia in Alaska and the Queen Charlotte Islands and their importance in the geographic co-occurrence of contact zones.

The importance of migration from Pleistocene refugia in the clustering of contact zones is even more evident in the southeastern United States. Here hot spots are abundant in Alabama, an area devoid of major mountains or other obvious barriers to dispersal (fig. 3). The co-occurrence of many contact zones in central Alabama is best explained as the outcome of contact between closely related species emerging from refugia located in Florida and east Texas–west Louisiana (see fig. 1; Parks et al. 1994;

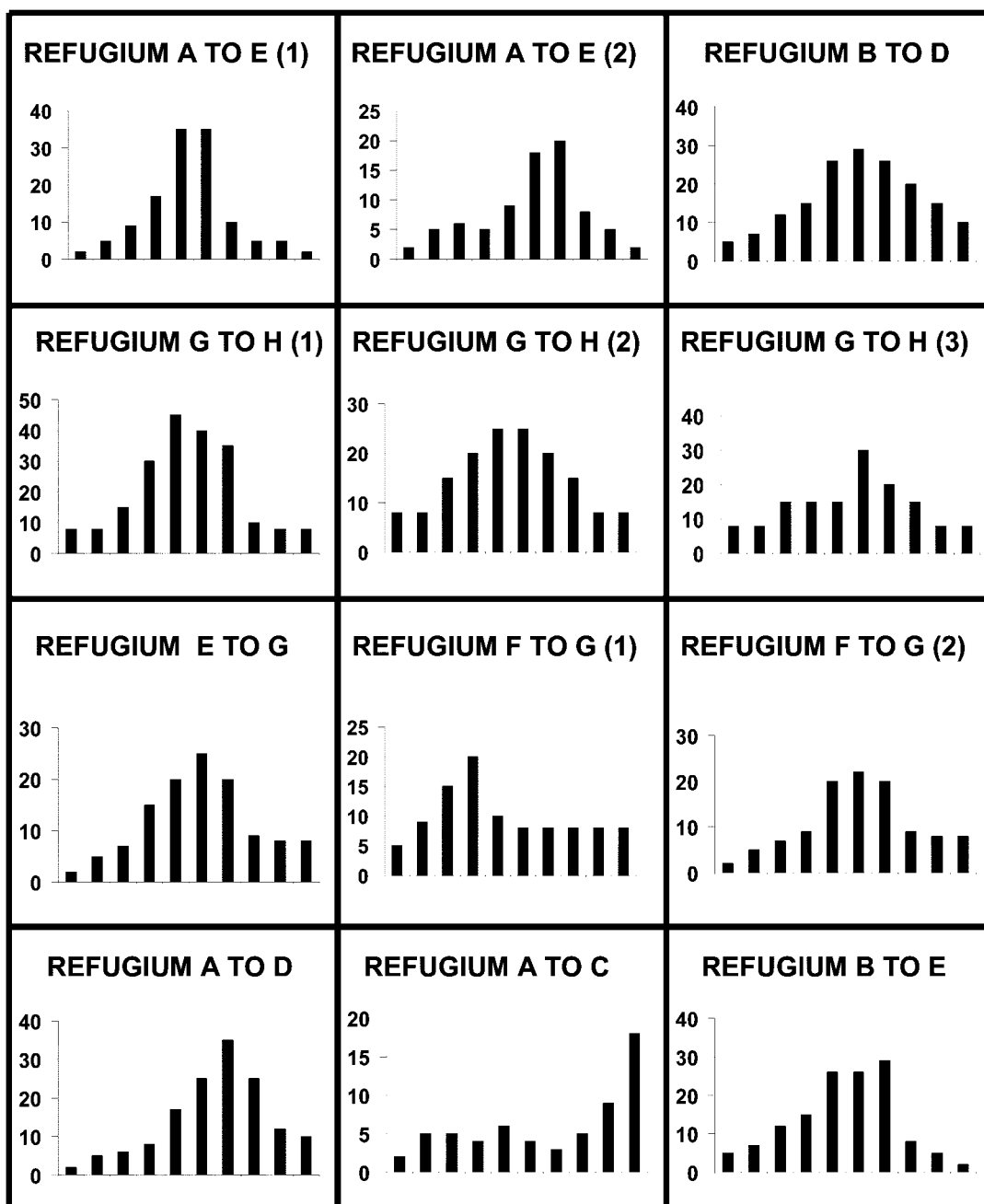


Figure 4: Histograms from contact zone distributional analyses: X-axis is linear location along the migration route and Y-axis is the number of contact zones. Numbers in parentheses refer to migration routes in a south-to-north orientation. Arrows depicting the meeting of routes B to D and A to E in Oregon are not shown in order to retain figure legibility. Refugia labeling corresponds to figure 1.

Sewell et al. 1996; Avise 2000), a scenario supported by histogram analyses (fig. 4).

The leading-edge hypothesis was invoked by Hewitt to explain the clustering of contact zones near the southern edge of the Wisconsin glacial maximum, such as the

hot spot near Lake Erie (Hewitt 2000). He suggests that the clusters in this area result from northern expansion of pairs of taxa and not the collision of pairs of taxa expanding out of two southern refugia. However, Austin et al. (2002, 2004) have suggested that phylogeographic

breaks in the spring peeper *Pseudacris crucifer* that have been found in this region are attributable to postglacial range expansion from refugia in Florida and Louisiana. We tested this hypothesis via histogram analysis (fig. 4), and our results support the expansion hypothesis of Austin et al. (2002, 2004). This finding underscores the difficulty of distinguishing between leading-edge and refugia scenarios.

Major rivers have long been seen as barriers to dispersal for terrestrial organisms (Wallace 1876; Pounds and Jackson 1981; Aleixo 2004). As such, one would expect borders between closely related species to show some association with rivers. However, the only contact zone hot spot in North America that may be accounted for by the presence of major rivers occurs along the Ohio and Mississippi Rivers near their confluence in southern Illinois (fig. 3).

The barriers and refugia that appear to account for clusters of contact zones in North America are the same factors that have been invoked to explain European suture zones (Hewitt 1996, 1999). Low mountain passes through the Pyrenees and Alps seem to have served as corridors of dispersal for taxa emerging from Iberian and Italian refugia, and many contact zones occur in these mountains. The hot spots in North American mountain chains (i.e., the Rocky Mountains) serve as an analogue to this European pattern. A central European suture zone initially identified by Remington (1968) and subsequently confirmed by Hewitt (1996, 1999) appears to be a meeting point for taxa emerging from refugia in the Balkans and the Iberian Peninsula. This zone represents a geographic midpoint suture zone similar to the suture zone exhibited in Alabama. Finally, suture zones in Northern Europe near the southern border of Pleistocene ice sheets suggest the possible action of a leading-edge process. This process may also help to account for some of the contact zone clustering that occurs in the Pacific Northwest region of North America.

How well do the contact zone hot spots identified in this study correspond to Remington's (1968) suture zones? The level of correspondence is similar to that seen in an earlier analysis that confined its attention to 117 hybrid zones studied in North America since 1970 (Swenson and Howard 2004). However, the enlargement of the contact zone data set through the addition of many new adjoining range boundaries and phylogeographic breaks provided support for more of Remington's individual suture zones. Six suture zones of Remington (1, 4, A, B, E, and G) showed a significant association with the contact zones mapped in this study, and three of the associations withstood a sequential Bonferonni correction (A, B, and E). In contrast, Swenson and Howard (2004) found support for only two of Remington's suture zones (1 and 4), and neither of these held up after sequential Bonferonni cor-

rection. It is interesting that the three suture zones best supported by the contact zone mapping carried out in this study were considered to be minor, rather than major, suture zones by Remington (1968). Minor suture zones were characterized as harboring fewer "known" hybrid zones than major suture zones; indeed, their delineations were based primarily on "suspected" hybrid zones.

Overall, it is difficult to escape the conclusion that contact zones between closely related taxa exhibit clustering in North America and that Remington correctly identified some of the areas where clustering occurs. The clear association of contact zone hot spots with mountain ranges, midpoints between refugia, and the southern edge of Pleistocene ice sheets emphasizes the importance of climate change and geographical barriers to dispersal in the evolution of species.

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