

NEWS AND VIEWS

PERSPECTIVE

Mapping the suturing of a continental biota

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The present-day spatial distribution of interspecific contact zones and intraspecific phylogeographical breaks provides a window into the past ecological and evolutionary processes that underlie speciation and species ranges. The clustering of contact zones and/or phylogeographical breaks in space indicates the suturing of diverged biotas. The presence of such suture zones indicates that similar ecological and historical factors have influenced the past and present distributions of populations and their divergence. Thus, suture zones are ideal natural laboratories for studying divergence, secondary contact and speciation across many different taxa. The concept of suture zones was formalized decades ago by Remington (1968), but only a few detailed and quantitative investigations of suture zones exist (Swenson & Howard 2004, 2005; Whinnett *et al.* 2005; Moritz *et al.* 2009). This limited number of investigations is largely because of a lack of detailed geographical data and sophisticated analytical tools. In this issue of *Molecular Ecology*, Rissler & Smith (2010) have accomplished a detailed investigation into the suturing of amphibian lineages in the United States which uses both detailed geographical data and sophisticated analytical methods. The work greatly enhances our knowledge of suture zones by extending previous work that has focused less on amphibians and by explicitly considering the relationship between species richness and suture zones.

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A primary advance supplied by the work of Rissler & Smith (2010) is their focus on only amphibians across the entire continent that has enabled the detection of novel amphibian-specific suture zones. Previous work by Swenson & Howard (2004, 2005) that aimed to test for the existence of Remington's original suture zones included all terrestrial taxa including amphibians, but the number of

amphibian phylogeographical breaks and hybrid zones utilized in these studies is far fewer than that reported in this issue by Rissler & Smith (2010). In particular, while providing additional support for the presence of a contact zone in northern California and Alabama, their work finds strong evidence for suturing in the Great Basin and Wisconsin (Fig. 5 in Rissler & Smith (2010))—two regions not previously considered suture zones. Interestingly, both of these regions were originally identified as likely suture zones by Remington (1968), thereby providing even greater support for the presence of suture zones (Fig. 1).

There are two key methodological issues in the work of Rissler & Smith (2010) that have helped provide further evidence for Remington's suture zones. First, use of the broader definition of suture zones proposed by Swenson & Howard (2005) that considers not simply hybrid zone clustering, but also the clustering of contact zones and phylogeographical breaks. The clustering of hybrid zones alone in North America only shows marginal support for Remington's suture zones (Swenson & Howard 2004). Through the examination of phylogeographical breaks and contact zones in unison, evidence for suturing is much clearer and often corresponds with Remington's suture zones. Conceptually, this makes more sense as the clustering of sister lineages suturing in space, no matter their date of divergence, is indicative of a suture zone and the presence of shared historical and contemporary processes across taxa. Importantly, previous tests of North American suture zones have been ambiguous with respect to whether the contact zone or hybrid zone was formed by sister lineages which complicates the issue. Rissler & Smith (2010) addressed this issue directly using two clades with well-resolved phylogenies to show that the location of suture zones is sensitive to whether only sister lineages are considered or not. Thus, examining only sister lineages should be preferred both conceptually and methodologically.

The second methodological advance was made by Rissler & Smith (2010) via their recognition that amphibian contact zones and phylogeographical breaks often cluster in areas with high species richness. This concordance between apparent suture zones and species richness raises the question of whether suture zones in these regions are 'real' or simply the consequence of having more species. For example, if 6% of the lineages in all regions suture with a sister lineage, areas with higher species richness levels will have a greater number of contact zones or phylogeographical breaks and therefore be more likely deemed a suture zone. Thus, gradients in species richness may complicate the issue of detecting suture zones. Rissler & Smith (2010) address this issue from two angles. One angle is to highlight that the concordance of species richness and clustering of contact zones and phylogeographical breaks is itself

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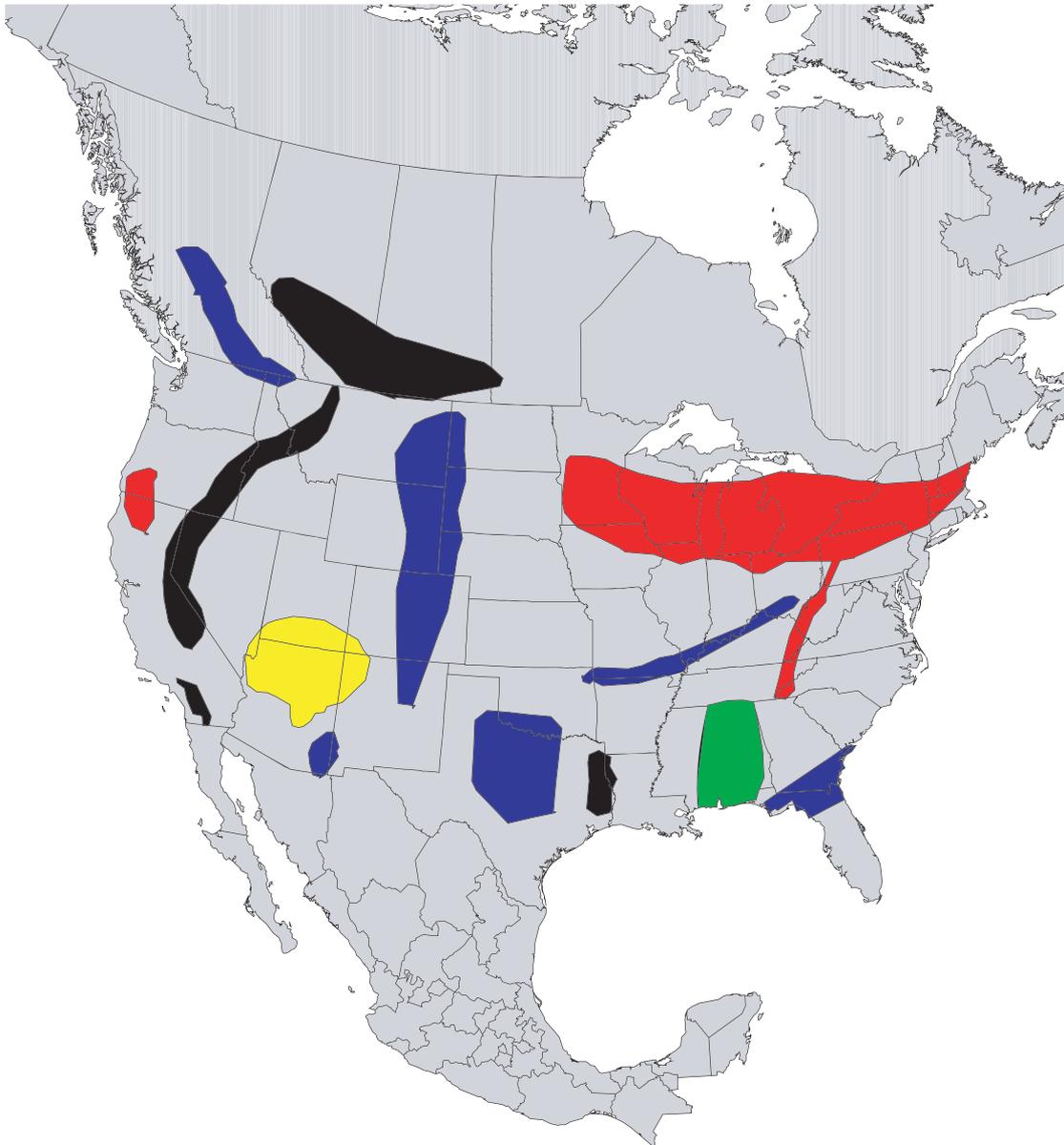


Fig. 1 A digital version of Remington's original suture zone map (Remington 1968). Suture zones coloured black have not been supported by modern spatial analyses. Suture zones coloured blue have been verified previously (Swenson & Howard 2004, 2005). Suture zones coloured red have been verified by Rissler & Smith (2010) and by Swenson & Howard (2004, 2005). Suture zones coloured yellow were not verified until the work by Rissler & Smith (2010). The green polygon indicates a suture zone not described by Remington (1968), but supported by extensive evidence from Rissler & Smith (2010) and Swenson & Howard (2005).

interesting. Indeed, the suturing of two separate biotas should increase the overall diversity of a location particularly if sister lineages can interdigitate spatially. The link between species richness and suture zones is also important from a conservation standpoint as these areas should be valued for their high levels of species richness and because they are wonderful natural laboratories for the study of speciation.

A second way in which Rissler & Smith (2010) address the link between species richness and apparent suture zones is by implementing a species richness correction. In

particular, the authors simply divide the number of contact zones and phylogeographical breaks found in a map grid cell by the number of species in that grid cell. This correction, while simple, standardizes the observed number of zones and breaks and provides a more robust answer to whether there are more zones and breaks in a map grid cell than that expected given the species richness. Interestingly, this correction procedure unveiled additional and previously unidentified amphibian suture zones (Fig. 1).

The correction procedure implemented by Rissler & Smith (2010) will help to propel a recent trend in phylogeog-

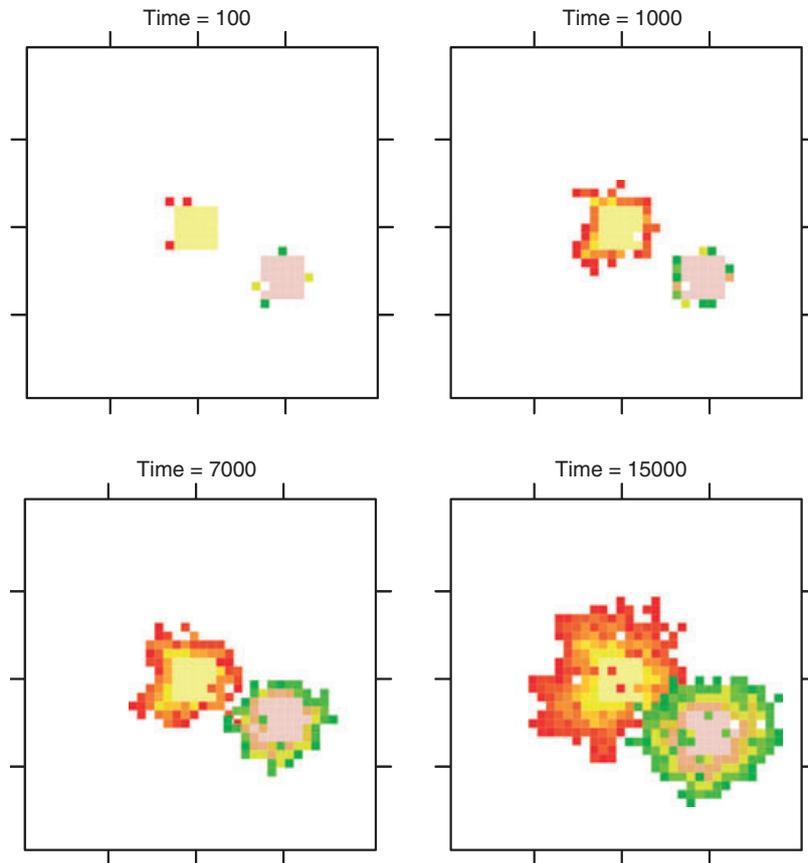


Fig. 2 An example of sister lineage range simulations using two-dimensional cellular automata. The basic idea is to randomly select two glacial refugia and grow the geographical ranges of the sister lineages as they expand out of their refugia. The final time step indicates present day where the total range overlaps of the two sister lineages can be calculated. This randomization or simulation procedure could be repeated hundreds or thousands of times to provide a null distribution of the expected number of phylogeographical breaks or sister lineage range overlaps within each map grid cell. Here, I have provided four time steps starting from 100 years after a glacial event where two sister lineages are isolated and ending at 15 000 years after a glacial event where the two sister lineages slightly overlap and suture.

graphical concordance research where spatial null models and corrections for underlying diversity gradients are being implemented. In particular, recent work by Soltis *et al.* (2006) and Moritz *et al.* (2009) has generated spatial null models to test for phylogeographical concordance and suture zones. Spatial null models such as these are critical for robust inferences regarding the spatial clustering of phylogeographical breaks and suture zones (Swenson 2008). Even stronger spatial null models can be generated in future work by utilizing macroecological cellular automata algorithms designed to simulate the geographical ranges of species given the observed range areas and land mass (Rahbek *et al.* 2007). These range simulations could be easily adapted to comparative phylogeography where the geographical ranges of lineages can be simulated thousands of times and an expected probability of phylogeographical break formation in each map grid cell in the study system can be estimated (Fig. 2).

Ultimately, the work by Rissler & Smith (2010) has advanced the study of suture zones greatly by providing an

in-depth investigation into a large and important clade of terrestrial vertebrates. Further, the authors have pushed the envelope on several analytical fronts and have provided another fine example of how large digital geographical data sets and sophisticated spatial analyses can advance the field of phylogeography. There is a bright future for the integration of geospatial technology and phylogeography, and the present work provides a window into that future.

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