

EDITORIAL

What is modern biogeography without phylogeography?



Somewhere around 26 years ago, I was beginning my doctoral research on the systematics and biogeography of grasshopper mice (genus *Onychomys*). I had fully intended to rely heavily on estimates of geographical variation derived from allozyme (protein) electrophoresis, which had become a method of choice among mammalogists during the 1970s for estimating genetic variation within and among closely related species. But before I began data collection in earnest, I stumbled upon a paper (Avice *et al.*, 1979) that used mitochondrial DNA (mtDNA) restriction fragment analyses to address geographical variation across the range of a species of pocket gopher (*Geomys pinetis*) in the south-eastern United States. I recall my epiphany upon seeing the level of resolution this method offered in not only defining and delineating geographically discrete western vs. eastern sets of populations, but also in how nicely the demarcation between groups seemed to be aligned with a plausible historical isolating event. I went on to read another mtDNA paper (Lansman *et al.*, 1983) that revealed surprising levels of geographical structure in the widespread North American rodent *Peromyscus maniculatus* – a species within a genus closely related to my own *Onychomys*. At that point there was no question that this new mtDNA-based assay of geographical variation was going to be my method of choice, and a very good one it turned out to be (see e.g. Riddle & Honeycutt, 1990).

While John Avice, along with his students and colleagues, continued throughout the 1980s to develop the theory behind and empirical utility of mtDNA-based assays of geographical structure in vertebrate species (Brown *et al.*, 1979; Brown, 1983; Wilson *et al.*, 1985) and chloroplast DNA (cpDNA) in plants (Palmer, 1985), ‘phylogeography’ was not described and defined formally until 1987 (Avice *et al.*, 1987). In over two decades since that seminal paper, phylogeography has blossomed – a November 2008 topic search of the ISI Web of Science using ‘phylogeograph*’ revealed 5076 studies to

date. Now phylogeography is not only a fundamental component of a core modern biogeography (Lomolino *et al.*, 2006), being employed across vertebrate, invertebrate, aquatic and terrestrial systems (as demonstrated in an exemplar set of papers bundled into a phylogeography section in this issue) – but perhaps just as importantly, is also an ever-expanding bridge between biogeography and related disciplines (Riddle *et al.*, 2008).

John Avice could be described as the ‘father of phylogeography’, and as such, he is the latest deserving recipient of the International Biogeography Society’s Alfred Russel Wallace Award for lifetime contributions to biogeography. In recognition of the sponsorship of this award by *Journal of Biogeography*, and as a lead-in to his scheduled keynote address at the January 2009 International Biogeography Society (IBS) conference in Mérida, Mexico, he has generously provided in this issue (Avice, 2009) a retrospective and prospective vision for phylogeography.

As Avice observes herein, phylogeography has traditionally emphasized, for good theoretical and empirical reasons, geographical variation in organellar genomes – mtDNA in animals and cpDNA in plants. It is generally acknowledged that mtDNA- or cpDNA-based studies have led to a revolution in our insights into the evolutionary and geographical responses of species and populations to (generally Quaternary and climatic) dynamics in Earth history (Zink & Barrowclough, 2008). However, legitimate concern has emerged over the extent to which organellar gene trees approximate the underlying organism or species tree (Edwards & Beerli, 2000), resulting in rapidly growing trends to develop, first, informative nuclear DNA loci (helped immensely by tapping into the databases being made available from whole genome-sequencing projects; Townsend *et al.*, 2008); and, second, multi-locus and multi-taxon analytical and computational approaches that can efficiently accommodate enormous and complex data sets (Hickerson *et al.*, 2007).

In a practical context, a key question for phylogeographers faced with limited resources will be how to optimize their sampling of individuals, localities and genes so as to recover the best obtainable signature of organism and biotic responses to events in Earth history; some answers should come from the continued development of multi-locus and multi-taxon coalescent theory and modelling, combined with a growing body of empirical studies.

Phylogeography has facilitated a revolution in the biodiversity sciences through its role in establishing the ‘microevolutionary–macroevolutionary’ nexus that Avice (2009) outlines in his Figure 2. I see a missing box, however, that should be nested within the Biogeography box in this figure in order to complete a more broadly satisfying depiction of the role of phylogeography within a modern biogeography. While I agree with the importance of the Phylogeography and Ecogeography boxes, I suspect that many of today’s biogeographers will wonder why there is not another box that draws from and informs the macroevolutionary disciplines, but additionally emphasizes historical patterns and processes above the levels of ‘conspecific organisms and closely related species’. I would redraw this figure to include a higher-taxon Historical biogeography box that incorporates concepts (and approaches based on them) such as areas of endemism, ancestral areas and the geography of speciation, and I would align these three boxes to form a triad, with double-headed arrows between all three. Further, I would expand the scope of the Ecogeography box beyond that reviewed by Gaston *et al.* (2008) to recognize the expanding role of biogeography in understanding, for example, community assembly and structure (Emerson & Gillespie, 2008). In my view, the critical role played by phylogeography would become even more relevant within this more inclusive vision of the purview of modern biogeography.

Finally, phylogeography promises to continue to play an important role in the expansion and integration of biogeography

with several emerging approaches and themes, including:

(1) Landscape genetics (Storfer *et al.*, 2007), which combines population genetics with principles of landscape ecology to examine population-level processes across increasingly fragmented landscapes, and is poised to take on an important role within the purview of conservation biogeography (Whittaker *et al.*, 2005).

(2) Ecological niche modelling (Waltari *et al.*, 2007), which uses current and palaeoclimatic modelling, along with palaeontology and 'phylochronology' (Hadly *et al.*, 2004), to generate and test hypotheses of shifting species distributions, population sizes, etc. across, for example, Late Glacial through Holocene time frames (Richards *et al.*, 2007).

(3) Phylogeographical information systems (Kidd & Ritchie, 2006), an approach to visualizing the geography of evolutionary diversification by building 3D 'geophylogenies' using gene and species trees in a GIS framework.

Biogeographers of all persuasions should embrace the remarkable success of phylogeography, and hence should thank John Avise for getting the ball rolling nearly three decades ago and playing a key role in nurturing it into the maturing discipline that continues to fill many pages of research journals in the biodiversity sciences (including this one). Biogeography is a richer science with the infusion of phylogeographical thinking and approaches, and one that is better prepared to address the future of biodiversity across the landscapes and seascapes of Earth.

BRETT R. RIDDLE

School of Life Sciences,
University of Nevada, Las Vegas,
4505 Maryland Parkway,
Las Vegas, NV 89154,
USA.

E-mail: brett.riddle@unlv.edu

REFERENCES

- Avise, J.C. (2009) Phylogeography: retrospect and prospect. *Journal of Biogeography*, **36**, 3–15.
- Avise, J.C., Giblin-Davidson, C., Laerm, J., Patton, J.C. & Lansman, R.A. (1979) Mitochondrial DNA clones and matrilineal phylogeny within and among geographic populations of the pocket gopher, *Geomys pinetis*. *Proceedings of the National Academy of Sciences USA*, **76**, 6694–6698.
- Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. & Saunders, N.C. (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.
- Brown, W.M. (1983) Evolution of animal mitochondrial DNA. *Evolution of genes and proteins* (ed. by M. Nei and R.K. Koehn), pp. 62–88. Sinauer, Sunderland, MA.
- Brown, W.M., George, M. & Wilson, A.C. (1979) Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences USA*, **76**, 1967–1971.
- Edwards, S.V. & Beerli, P. (2000) Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution*, **54**, 1839–1854.
- Emerson, B.C. & Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, **23**, 619–630.
- Gaston, K.J., Chown, S.L. & Evans, K.L. (2008) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, **35**, 483–500.
- Hadly, E.A., Ramakrishnan, U., Chan, Y.L., van Tuinen, M., O'Keefe, K., Spaeth, P.A. & Conroy, C.J. (2004) Genetic response to climatic change: insights from ancient DNA and phylochronology. *PLoS Biology*, **2**, 1600–1609.
- Hickerson, M.J., Stahl, E. & Takebayashi, N. (2007) msBayes: Pipeline for testing comparative phylogeographic histories using hierarchical approximate Bayesian computation. *BMC Bioinformatics*, **8**, 268.
- Kidd, D.M. & Ritchie, M.G. (2006) Phylogeographical information systems: putting the geography into phylogeography. *Journal of Biogeography*, **33**, 1851–1865.
- Lansman, R.A., Avise, J.C., Aquadro, C.F., Shapira, J.F. & Daniel, S.W. (1983) The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. 4. Extensive genetic variation in mitochondrial DNAs among geographic populations of the deer mouse, *Peromyscus maniculatus*. *Evolution*, **37**, 1–16.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006) *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.
- Palmer, J.D. (1985) Evolution of chloroplast and mitochondrial DNA in plants and algae. *Molecular evolutionary genetics* (ed. by R.J. MacIntyre), pp. 131–240. Plenum Press, New York.
- Richards, C.L., Carstens, B.C. & Knowles, L.L. (2007) Distribution modelling and statistical phylogeography: an integrative framework for generating and testing alternative biogeographical hypotheses. *Journal of Biogeography*, **34**, 1833–1845.
- Riddle, B.R. & Honeycutt, R.L. (1990) Historical biogeography in North American arid regions: an approach using mitochondrial-DNA phylogeny in grasshopper mice (genus *Onychomys*). *Evolution*, **44**, 1–15.
- Riddle, B.R., Dawson, M.N., Hadly, E.A., Hafner, D.J., Hickerson, M.J., Mantooth, S.J. & Yoder, A.D. (2008) The role of molecular genetics in sculpting the future of integrative biogeography. *Progress in Physical Geography*, **32**, 173–202.
- Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L. & Waits, L.P. (2007) Putting the 'landscape' in landscape genetics. *Heredity*, **98**, 128–142.
- Townsend, T.M., Alegre, R.E., Kelley, S.T., Wiens, J.J. & Reeder, T.W. (2008) Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles. *Molecular Phylogenetics and Evolution*, **47**, 129–142.
- Waltari, E., Hijmans, R.J., Peterson, A.T., Nyari, A.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*, **2**, e563.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation Biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.
- Wilson, A.C., Cann, R.L., Carr, S.M., George, M., Gyllenstein, U.B., Helmbachowski, K.M., Higuchi, R.G., Palumbi, S.R., Prager, E.M., Sage, R.D. & Stoneking, M. (1985) Mitochondrial DNA and two perspectives on evolutionary genetics. *Biological Journal of the Linnean Society*, **26**, 375–400.
- Zink, R.M. & Barrowclough, G.F. (2008) Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, **17**, 2107–2121.