



## Phylogeography

This issue is dedicated to phylogeography, a relatively young research field dating back to some 30 years. The field was sculpted by John Avise's book 'Phylogeography' (Avise, 2000), and the subsequent rapid developments in molecular techniques which facilitate a rapid, cheap and accurate documentation of genetic differentiation across many populations. This was paralleled by better analytical tools. In the last decade, phylogeography has become a major component of biogeography. Phylogeographical methods have been used to address many questions. The major achievements of Avise and colleagues were illustrating shared biogeographical patterns in freshwater, terrestrial and marine taxa in SE USA; meanwhile, on the other side of the Atlantic, phylogeographical studies made major progress in elucidating Late Quaternary range contractions and expansions in Europe. The remarkable success of phylogeographical methods in disentangling the Late Quaternary history of the European biota stimulated similar studies in many parts of the globe, terrestrial and marine. It also led to the asking of more complex questions, integrating ecology and history. The collection of papers in this issue does not cover the full breadth of issues addressed using phylogeographical methods, but it does give a taste of what is possible.

The search for refuges (typically, where species survived periods when the climate was less suitable) and range expansion patterns is still a very common theme in phylogeographical studies, and is also the focus of many papers in this issue, covering Arctic to tropical as well as terrestrial and marine species. Gutiérrez-Rodríguez *et al.* (2017) demonstrate southern Iberian refuges with northern expansion for the spadefoot toad, matching species distribution models, with patterns of genetic diversity. Alexandri *et al.* (2017) continued their exploration of Balkan refuges for wild boar,

showing differences between microsatellite and genome-wide SNP analyses. Han-temirova *et al.* (2017) showed that far northern Russian and Siberian populations of the common juniper are largely descendent from populations which survived in cryptic northern refuges, and that the contribution of southern refuges to these populations was relatively small, thus upsetting the paradigm of southern refuges. The region(s) where the Aleutian flora survived the Last Glacial Maximum (LGM) is still unknown, and Hata *et al.* (2017) showed that *Therorhodon camtschaticum* (Ericaceae) probably survived the LGM on Kamchatka. The evolution of the enormous diversity of the Hengduanshan Biodiversity Centre is still enigmatic. Du *et al.* (2017) explored the phylogeography of one of the woody species in the region, *Quercus aquiloides*, and showed that in Tibet, the species presence was dynamic, whereas in the Hengduan Mountains, populations were stable, and that this stability is associated with a high haplotype diversity. It has long been suggested that during the LGM, the African tropical rain forests were restricted to few refugia, and Ley *et al.* (2017) demonstrate that the genetic patterns in the liana *Haumania* are consistent with these refuges with subsequent range expansion and admixture. The climate in deserts also fluctuated during the Late Quaternary, and Scheinvar *et al.* (2017) showed that *Agave lechuguilla* survived the LGM in five refuges in the North American Chihuahuan desert from which it expanded during the Holocene. Spatial genetic structure in marine organisms is also consistent with fluctuating climates, illustrated for red mangroves in Florida (comparing the east and west coasts) by Kennedy *et al.* (2017), and for Atlantic starfish by Pérez-Portela *et al.* (2017). These case studies add to the detailed understanding, developed over the past decade, of the biotic responses to Quaternary climatic fluctuation.

There are some interesting complications to these patterns. Fang *et al.* (2017) showed that the genetic patterns were

strongly influenced by the reproductive biology in two aphid species which feed on the same species of Chinese willow, but which have different life cycles, with the sexual species with more genetic and population variation than the asexual species. Llorens *et al.* (2017) demonstrated that the wind pollinated Australian shrub, *Allocasuarina humilis*, showed no regional genetic structure, indicative of populations that have had their current distribution for a long time, but that genetic structure was influenced by the degree of population fragmentation. Another form of intrinsic genetic variation was shown by McMinn *et al.* (2017): marginal populations were genetically less variable than central populations in *Cirsium canescens* in North America.

Simplistically, spatial genetic structure in a species is due to either adaptation or historical factors, but the two are rarely combined. Such a combination combines the fields of trait and historical biogeography. Polfus *et al.* (2017) explore this link between ecotypes and genetic lineages in Canadian caribou, and Díaz *et al.* (2017) between the distribution of cryptic coloration and genetic lineages in an Iberian lizard.

Islands also generate phylogeographical pattern, for example, in the Indian Ocean geckos (Hawltischek *et al.*, 2017). Such patterns can persist long after the ocean has retreated, leaving previous islands as modern mountains, as illustrated for a Carpathian crustacean (Copilaş-Ciocianu & Petrusek, 2017), restricted to mountains that formed an archipelago in the European Miocene epicontinental sea.

Phylogeographical patterns are often taxonomy informative (Avise, 2000). Habel *et al.* (2017) combined morphological data with genetically informed phylogeographical methods to evaluate the divergence in the marbled butterfly species group in the Western Palaearctic. The documentation of the phylogeographical patterns in starfish in the Atlantic and Mediterranean Pérez-Portela *et al.* (2017) also led to the recognition of two species separated by oceanic currents.

Finally, a criticism of many phylogeographical studies is that they apply only to one species, and so have no generality. Comparative phylogeography, where the responses of many lineages to the same barrier are explored, is one way of seeking general phylogeographical patterns. This approach is illustrated here by Myers *et al.* (2017), who show an asynchronous differentiation across the same North American interval by several snake lineages. The challenge in comparative phylogeographical studies is obtaining sufficient data, and Gratton *et al.* (2017) explore the possibility of using the enormous resources already available on Genbank to this end. Frustratingly, although the methods work, there are still very few georeferenced sequences on Genbank.

In combination, this collection of papers, reporting on studies from almost all continents, illustrates the enormous range of questions that can be addressed with phylogeographical methods. There are still many other questions waiting to be addressed, ranging from the impact of the south-central African mega-droughts (Lyons *et al.*, 2015) to a more general understanding of the links between trait and phylogeographical variation. Equally exciting is the development of new methods, from genomic (next generation sequencing) approaches to high resolution remote sensing, which may facilitate phylogeographical research. We are looking forward to being able to publishing many more exciting phylogeographical papers.

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## REFERENCES

- Alexandri, P., Megens, H.-J., Crooijmans, R.P.M.A., Groenen, M.A.M., Goedbloed, D.J., Herrero-Medrano, J.M., Rund, L.A., Schook, L.B., Chatzinikos, E., Triantaphyllidis, C. & Triantafyllidis, A. (2017) Distinguishing migration events of different timing for wild boar in the Balkans. *Journal of Biogeography*, **44**, 259–270.
- Avise, J.C. (2000) *Phylogeography*. Harvard University Press, Cambridge, Massachusetts, The history and formation of species???
- Copilaş-Ciocianu, D. & Petrusek, A. (2017) Phylogeography of a freshwater crustacean species complex reflects a long-gone archipelago. *Journal of Biogeography*, **44**, 421–432.
- Díaz, J.A., Verdú-Ricoy, J., Iraeta, P., Llanos-Garrido, A., Pérez-Rodríguez, A. & Salvador, A. (2017) There is more to the picture than meets the eye: adaptation for crypsis blurs phylogeographical structure in a lizard. *Journal of Biogeography*, **44**, 397–408.
- Du, F.K., Hou, M., Wang, W., Mao, K. & Hampe, A. (2017) Phylogeography of *Quercus aquifolioides* provides novel insights into the Neogene history of a major global hotspot of plant diversity in south-west China. *Journal of Biogeography*, **44**, 294–307.
- Fang, F., Chen, J., Jiang, L.-Y., Chen, R. & Qiao, G.-X. (2017) Biological traits yield divergent phylogeographical patterns between two aphids living on the same host plants. *Journal of Biogeography*, **44**, 348–360.
- Gratton, P., Marta, S., Bocksberger, G., Winter, M., Trucchi, E. & Köhl, H. (2017) A world of sequences: can we use georeferenced nucleotide databases for a robust automated phylogeography? *Journal of Biogeography*, **44**, 475–486.
- Gutiérrez-Rodríguez, J., Barbosa, A.M. & Martínez-Solano, Í. (2017) Present and past climatic effects on the current distribution and genetic diversity of the Iberian spadefoot toad (*Pelobates cultripes*): an integrative approach. *Journal of Biogeography*, **44**, 245–258.
- Habel, J.C., Vila, R., Vodá, R., Husemann, M., Schmitt, T. & Dapporto, L. (2017) Differentiation in the marbled white butterfly species complex driven by multiple evolutionary forces. *Journal of Biogeography*, **44**, 433–445.
- Hantemirova, E.V., Heinze, B., Knyazeva, S.G., Musaev, A.M., Lascoux, M. & Semerikov, V.L. (2017) A new Eurasian phylogeographical paradigm? Limited contribution of southern populations to the recolonization of high latitude populations in *Juniperus communis* L. (Cupressaceae). *Journal of Biogeography*, **44**, 271–282.
- Hata, D., Higashi, H., Yakubov, V., Barkalov, V., Ikeda, H. & Setoguchi, H. (2017) Phylogeographical insight into the Aleutian flora inferred from the historical range shifts of the alpine shrub *Therorhodon camtschaticum* (Pall.) Small (Ericaceae). *Journal of Biogeography*, **44**, 283–293.
- Hawiltschek, O., Toussaint, E.F.A., Gehring, P.-S., Ratsoavina, F.M., Cole, N., Crottini, A., Nopper, J., Lam, A.W., Vences, M. & Glaw, F. (2017) Gecko phylogeography in the Western Indian Ocean region: the oldest clade of *Ebenavia inunguis* lives on the youngest island. *Journal of Biogeography*, **44**, 409–420.
- Kennedy, J.P., Garavelli, L., Truelove, N.K., Devlin, D.J., Box, S.J., Chérubin, L.M. & Feller, I.C. (2017) Contrasting genetic effects of red mangrove (*Rhizophora mangle* L.) range expansion along West and East Florida. *Journal of Biogeography*, **44**, 335–347.
- Ley, A.C., Heuertz, M. & Hardy, O.J. (2017) The evolutionary history of central African rain forest plants: phylogeographical insights from sister species in the climber genus *Haumania* (Marantaceae). *Journal of Biogeography*, **44**, 308–321.
- Llorens, T.M., Tapper, S.-L., Coates, D.J., McArthur, S., Hankinson, M. & Byrne, M. (2017) Does population distribution matter? Influence of a patchy versus continuous distribution on genetic patterns in a wind-pollinated shrub. *Journal of Biogeography*, **44**, 361–374.
- Lyons, R.P., Scholz, C.A., Cohen, A.S., King, J.W., Brown, E.T., Ivory, S.J., Johnson, T.C., Deino, A.L., Reinthal, P.N., McGlue, M.M. & Blome, M.W. (2015) Continuous 1.3-million-year record of East African hydroclimate, and implications for patterns of evolution and biodiversity. *Proceedings of the National Academy of Sciences USA*, **112**, 15568–15573.
- McMinn, R.L., Russell, F.L. & Beck, J.B. (2017) Demographic structure and genetic variability throughout the distribution of Platte thistle (*Cirsium canescens* Asteraceae). *Journal of Biogeography*, **44**, 375–385.
- Myers, E.A., Hickerson, M.J. & Burbrink, F.T. (2017) Asynchronous diversification of snakes in the North American warm deserts. *Journal of Biogeography*, **44**, 461–474.
- Pérez-Portela, R., Rius, M. & Villamor, A. (2017) Lineage splitting, secondary contacts and genetic admixture of a widely distributed marine invertebrate. *Journal of Biogeography*, **44**, 446–460.
- Polfus, J.L., Manseau, M., Klütsch, C.F.C., Simmons, D. & Wilson, P.J. (2017) Ancient diversification in glacial refugia leads to intraspecific diversity in a Holarctic mammal. *Journal of Biogeography*, **44**, 386–396.
- Scheinvar, E., Gámez, N., Castellanos-Morales, G., Aguirre-Planter, E. & Eguarte, L.E. (2017) Neogene and Pleistocene history of *Agave lechuguilla* in the Chihuahuan Desert. *Journal of Biogeography*, **44**, 322–334.