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Rakesh Kumar & Vinod Kumar

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A review of phylogeography: biotic and abiotic factors

Rakesh Kumar and Vinod Kumar

Department of Botany, DAV University, Jalandhar, India

ABSTRACT

Phylogeography expounds population genetics and phylogenetics in straightforward geographic manner, providing good framework in revealing the evolutionary background of the species. It also records the spatial distribution of genetic lineages which are outcome of population structure mechanisms such as population contraction, population expansion, gene movements and climatic oscillations shaped by climate fluctuations and the physical landscape. The environmental heterogeneity abets organism colonization into new sites and induces adaptive genetic changes in them by creating separation at specific loci. Phylogeography encodes the spatial and temporal distribution of population structure in relation to their ecological and biological requirements which can decipher evolutionary processes. Modern tools that generate genome-wide sequence data are now available which allow us to understand how evolutionary processes affect the spatial distribution of different kinds of individuals and also to model the future spatial distribution of species with respect to climate change.

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1. Introduction

Phylogeography is an important branch of science which uses genetic information to investigate the geographical distribution of genealogical lineages, mainly those located within the species (Avise, 2000). It aims at depicting the patterns of geographic dispersal of taxa and understanding the mechanisms responsible for their varied distribution (Frederico, Farias, Araújo, Charvet-Almeida, & Alves-Gomes, 2012). The deepest levels of phylogeographical partitioning are linked with geological or pre-quaternary climatic changes and isolation by distance. Even the subtle environmental changes substantively affect the process of phylogeography by modulating the natural selections within divergent climates. Phylogeography certifies the spatial dispersal of genetic lineages that results due to population expansion, population contraction and gene movements. Most of the phylogeographic studies used neutral markers, however not too much emphasis is given to the role of selection in phylogeography (Sork et al., 2016). Wiantoro, Maryanto, and Abdullah (2012) studied the phylogeography of *Myotis muricola* from west and east of Wallace's line using partial mitochondrial DNA *cyt b* gene and concluded that species exhibit some degree of population structure that can be analyzed in geographic and sequential contexts. Interpreting the spatial and temporal elements of population structure and deciphering the ecological and biological elements are important for phylogeography.

Based on individuals and genes sampling, the phylogeographers can propose biogeographic hypothesis, which deciphers the evolutionary path of reproductive isolation of population units along with the underlying mechanism of their origin and distribution. By providing the structure of population ancestors which is affected by demographic history, phylogeographers can also predict the temporal variations in the physical and biotic environment of the population, prevailing in those times, using present day genetic data. For such purposes, phylogeography has contributed a lot in many areas of biology and earth sciences, i.e., speciation, historical biogeography, human evolution, biodiversity research and taxonomy and volcanology (Avise, Walker, & Johns, 1998; Beaumont, 2004; Emerson, 2002; Kohn, 2005; Riddle & Hafner, 2006; Templeton, 2005; Torroni, Achilli, Macaulay, Richards, & Bandelt, 2006). Species which are adjusted to temperate regions have reacted to glaciations by following a phylogeographic pattern, where range of species contracts during Pleistocene glaciations into southern refugia positioned in the region of Mediterranean peninsulas and afterwards the population increased into the other regions of the continent during interglacial (Petit et al., 2003). This contraction-expansion has been opposed as various studies have recommended that refugia were not limited to the southern regions, but also present in the western, eastern and central Europe, mostly as local northern or cryptic refugia (Bartha et al., 2015; Schmitt & Varga, 2012; Stewart &

Lister, 2001). In the present review, we emphasize on the various biotic and abiotic factors of the phylogeography.

2. Phylogeographic factors

Phylogeographic distribution of organism is affected by a number of biotic and abiotic factors. These factors decide the abundance of particular species in concerned area. Some of the biotic and abiotic factors are responsible for varied phylogeographic patterns as explained as under.

2.1. Abiotic factors

Different abiotic factors have affected the speed and shape of evolutionary processes. Some of these are mentioned below:

2.1.1. Topographic variations

The topographical variations shaped over a long period of time have resulted in diverse phylogeographic patterns. Some of the major factors responsible for such patterns are phylogeographic breaks, latitudinal gradient, glacial refuge and geographic position of straits.

2.1.2. Phylogeographic breaks

These geographical separations might have resulted due to the contraction of previous continuous areas. The “refugia within refugia” model was proposed to explain phylogeographic breaks responsible for preservation of lineages within peninsula (Gómez & Lunt, 2007). Researchers studied the comparative phylogeography of black and red mangroves in Florida (Hodel, de Souza Cortez, Soltis, & Soltis, 2016). They found higher dispersal rate was key of success for one species. A complex evolutionary history of threatened cloud forest of Northern Mesoamerica was observed by Ornelas et al. (2013). They observed shared phylogeographic breaks which relate to the Isthmus of Tehuantepec, Los Tuxtlas, and the Chiapas Central Depression. Their dating analyses advocated that the phylogeographic breaks corresponding to the Isthmus occurred at different times in different taxa. The Phylogeography of Missouriensis was investigated by Cornman and Arnold (2007) and was found to be based upon nuclear and chloroplast markers. Although the physiological breaks do not correspond to gaps found in present distribution, but they do represent a measure of reproductive isolation.

2.1.3. Latitudinal gradient

As we move from poles to equator, the latitudinal gradient shows different biodiversity patterns. This pattern shows north-south decrease in genetic variation. This change in patterns has been mathematically explained with the help of various models like leading edge expansion model and successive variance models. The diversity and distribution of freshwater aerobic an oxygenic phototrophic bacteria (AAPs) was explored in the lakes

along the latitudinal gradient (Ferrera et al., 2017). They observed distribution patterns of AAPs along the latitudinal gradient which might be due to the small-scale environmental conditions formed along the axis. The only impediment to assess the dynamics of latitudinal diversity gradient is the tendency to focus narrowly on single casual factor when a more integrative approach is required (Jablonski, Huang, Roy, & Valentine, 2017).

2.1.4. Glacial refuge

Glacial refuges are areas which have served reservoir of flora and fauna in times of ice ages and permitted post glacial establishment of species. The forest refuge hypothesis (FRH) has been perfect model for explaining the large biodiversity of tropical forests. According to FRH, the retraction and fragmentation of forests during glacial periods induced reproductive isolation and concomitantly giving rise to speciation in small forest patches which are surrounded by large opens spaces (Leite et al., 2016). Hewitt had put forward a model (paradigm postglacial colonization patterns) which explained a single refugium as the source of recolonization (Hewitt, 2000). Pulido-Santacruz, Bornschein, Belmonte-Lopes, and Bonatto (2016) studied multiple evolutionary units and demographic stability during the last glacial maximum in the *Scytalopus peluncae* complex. Their results attributed the stable nature Atlantic forests in maintaining endemic species due to glacial cycles operating in it.

2.1.5. Geographic position of straits

Strait is defined as naturally formed narrow, navigable water channel between two land masses. Strait of Gibraltar and Pyrenees of Alps are examples of great biogeographical barriers. Strait of Gibraltar has posed a brier for continental *Juniperus thurifera*, *Carex helodes*, *Abies* spp. Still their role as barrier to gene flow has been questioned by a number of authors as they allow occasional communication. The effectiveness of strait to act as a barrier depends upon a number of factors like its position, width and depth (Rodríguez-Sánchez, Pérez-Barrales, Ojeda, Vargas, & Arroyo, 2008).

2.1.6. Climatic oscillations

The unpredictable global climatic changes in the past 2 million years have resulted in abrupt and unforeseen environmental changes that have hugely affected the geographical distribution of plant species worldwide (Qiu, Fu, & Comes, 2011). The long-term changes such as gradual cooling since Oligocene and aridification (9–8 million years ago) has shaped the palaeoclimatic history of Mediterranean Basin (Zachos, Dickens, & Zeeb, 2008). The late Miocene has witnessed subduction process in Westernmost Mediterranean which has broken of contact between Atlantic Ocean and Mediterranean sea resulting Messinina salinity crisis (drying up of Mediterranean sea) (Hsü, 1972; Krijgsman, 2002).

This period was trailed by creation of Mediterranean-type climate around 3.2 million years ago (Suc, 1984). Further, the Milankovitch oscillations has influenced the Basin by cyclic climatic changes by affecting the periodical shift in earth's orbit and axil tilt, thereby decreasing their periodicity to 100 ky during the Pleistocene (Jansson & Dynesius, 2002). The genetic composition of Mediterranean flora has been shaped by westward or eastward waves of colonization. This happened not just during Pleistocene but at varied times depending upon ecological requirements and climatic conditions of species in question (e.g., Araceae, *C. extensa*, *Erica arborea* and *M. communis* (Désamoré et al., 2011; Escudero, Vargas, Arens, Ouborg, & Luceño, 2010; Mansion et al., 2008; Migliore, Baumel, Juin, & Médail, 2012). The recent speciation events accompanying climatic change in Pleistocene have contributed to the biodiversity as compared to Cape Flora (Valente & Vargas, 2013). These oscillations in Pleistocene climate have been explained by vicariant model. This model explained that during interglacial period, the winter adapted species got fragmented and restricted to higher elevations (e.g., herbaceous perennials such as *Pritzelago alpina* (L.) Kuntze, *S. rupestris*, *G. alpina*, *K. saxatilis*, *S. oppositifolia* (Kropf, Comes, & Kadereit, 2006, 2008; Kropf, Kadereit, & Comes, 2003), *Androsace vitaliana* (L.) Lapeyr. (Dixon, Schönschwetter, Vargas, Ertl, & Schneeweiss, 2009), Resedaceae. *Glaucoreseda* (Martín-Bravo, Valcárcel, Vargas, & Luceno, 2010) as well as trees such as *Pinus mugo* Turra (Heuertz et al., 2010). The earth has encountered large, abrupt and widespread climatic changes in the past. These climatic changes are result of many reasons, but major challenge is posed by humans now a days. The latter are inducing similar changes but at faster rate. The reoccurrence of such events in the present era will have a much larger economic and ecological impact. The climatic changes being most of the times unpredictable will always be associated with uncertainties. The research should be focused on updating monitoring systems, increasing adaptability and resilience of ecosystems (Alley et al., 2003).

2.2. Biotic factors: Various biotic factors are responsible for phylogeography are as under:

2.2.1. Population expansion

Population expansion means the spread of population over space (Bosch, Metz, & Diekmann, 1990). Many authors have studied the population expansion strategies of various plants and animal species. However, it is difficult to study the population expansion of trees as their life span is very long, but still there are methods like radiocarbon dating which solve this problem to some extent are available (Bennett, 1983). Researchers studied population expansion and successive isolation stimulated morphological heterogeneity in *Rosa sericea* complex (Gao, Zhang, Gao, & Zhu, 2015). They studied

three chloroplast DNA fragments such as *ndhJ-trnF*, *trnL-trnF* and *ndhF-rpl32* and nuclear microsatellite to confirm whether cold tolerant plants accomplished expansion during the Pleistocene. The role of postglacial population expansion on phylogeography of Nearctic songbird was studied in 2000 (Mila, Girman, Kimura, & Smith, 2000). Samples from 12 breeding locations in USA and two locations in north-eastern Mexico were selected as study area. The study showed indications of late pleistocene population expansions due to low haplotypes and nucleotide diversity, star like phylogeny of alleles and mismatch dispersal revealing a prompt increase in population size. However, later showed high genetic diversity and mismatch dispersal as imagined for a population unchanged by prompt demographic variation. These observations supported the fact that postglacial expansion of bottlenecked population may be an explanation to absence of structure and variation found for most North American songbird species. The mitochondrial DNA control region sequencing was used to study the phylogeography of the rodent *Ctenomys australis* (Mora, Lessa, Kittlein, & Vassallo, 2006). Similar studies were also conducted on the phylogeography of four samples of *S. sarda*. They found two clades almost 8.1% divergent dispersed in the east west cline (Vinas, Bremer, & Pla, 2004). Changes in clade I indicate large stable population and clade II suggests a star like phylogeny representative of population bottleneck followed by prompt population expansion. The phylogeography of *Thunnus thynnus* and *Xiphias gladius* as studied by the researchers in 2005 was an interesting study (Bremer, Viñas, Mejuto, Ely, & Pla, 2005). In spite of their opposite phylogenetic and phylogeography, the population of *T. thynnus* and *X. gladius* recommends concordance in timeline of population expansion. Phylogeography of *Lipophrys pholis* was studied by using a fragment of mitochondrial control region and first intron of S7 ribosomal protein gene. The genealogy of European population indicated that the largest population expansion found was older than the last glaciations (Francisco et al., 2011). Two chloroplast regions such as *trnS-trnG* and *rpl32-trnL* were used to study the phylogeography of *Palicourea padifolia* (Gutiérrez-Rodríguez, Ornelas, & Rodríguez-Gómez, 2011). The pattern of geographic structure showed by this work is constant with past fragmentation and population structure range expansion. Investigations on the phylogeographic relationships of *Alces alces* globally to check the proposed existence of two geographic races and to conclude the timing and extent of demographic processes supported the expansion of *Alces alces* across the Northern Hemisphere in late Pleistocene (Hundertmark et al., 2002).

2.2.2. Population contraction

The decrease in population of an organism is called population contraction. There are number of factors responsible for it, e.g., loss of habitat, sharp changes

in the environment and various other anthropogenic factors (Hu, Qi, Wang, & Wei, 2010). Numerous mathematical models are available to study the population contraction like hierarchical Bayesian model, correlative species distribution model so on and so forth. Using the above-mentioned mathematical model, the alternative hypothesis about historical changes of population contraction and expansion in *Cynopterus sphinx* and *C. brachyotis* using coalescent-based investigation of microsatellite change was done (Storz & Beaumont, 2002). The analysis suggested that population of both species contracted. This may be expected that biogeographic consideration responsible for population contraction in *Cynopterus sphinx*. The phylogeography of *Bombus morio* and *B. pauloensis* in Atlantic forest and Brazilian savannas was studied using correlative species distribution model (Françoso, Zuntini, Carnaval, & Arias, 2016). Results indicated that warmer conditions of the last interglacial-induced population contraction. The phylogeography of *Podarcis siculus* was studied using mitochondrial cyt b, nuclear *mclr* and *β-fibint* 7 genes (Senczuk, Colangelo, De Simone, Aloise, & Castiglia, 2017). The population level historical demography showed a trend constant with glacial expansion and regional determination during the last glacial maximum. This genetic complex appears to be unchanged with the expectation of the expansion–contraction model and post-last glacial maximum from Southern refugia. The cyclic population contractions and expansions advised by the quaternary climatic oscillation are regarded as one of the major significant processes that led to current dispersal of genetic variation across different geographic regions (Hickerson et al., 2010; Provan & Bennett, 2008; Schmitt, 2007). Moreover, large amount of molecular data led to broad flexibility of the expansion–contraction model of Pleistocene biogeography (Hewitt, 1996) and expectations of the post-last glacial maximum population structure expansions from Southern refugia. These new aspects indicate that some temperate species could experience attenuated or changed responses to glacial population contractions with the absence of post-last glacial maximum recolonization system (Bisconti, Canestrelli, Colangelo, & Nascetti, 2011; Salvi, Schembri, Sciberras, & Harris, 2014). Quaternary climatic changes restructured biodiversity across North American high latitudes through repeated episodes of range contractions, population isolation and separation, and finally expansion. Using multilocus method under a Bayesian Coalescent framework, the phylogeography of a broad-ranged mammal, long-tailed vole, *Microtus longicaudus* were studied by Sawyer and Cook (2016). In this study, an expansion–contraction model was tested on the *C. elaphus* using modern as well as ancient mitochondrial DNA.

2.2.3. Gene movements

The gene movement means the transfer of genes within species or from one species to other. This movement of genetic information plays an important role in phylogeography of organisms. *Ichthyophis bannanicus* is the only Caecilian species in China whose phylogeographical and population structure was studied. The study recognized that Red river and Pearl river systems may act as gene flow hurdle for *I. bannanicus* (Wang et al., 2015). Lai et al. (2004) studied the loss and movements of genes in maize genome. To explore the fate of its gene after tetraploidization, they studied sequence of five duplicated locations from various chromosomal sites. By scoring the region from each maize plant individually, the non-collinear genes set from all the four sites jumped to 68%. Due to this, approximately 50% of the duplicated genes from two ancestors of maize have lost within a short span of time. This indicated that many genes were moved to new chromosomal regions in the last 50 million years. Ming et al. (2016) studied the genetic diversity of *Camelus bactrianus* and *C. ferus* by examining 809 bp mitochondrial DNA fragment from 113 individuals, indicating eleven domestic breeds, one wild breed and two hybrid individuals. They reported 15 different haplotypes and the phylogenetic study revealed that wild and domestic Bactrian Camels have two different lineages. The study of domestic *C. bactrianus* from various sites indicates that, there was no significant separation in Russia, Mongolia and China. This observation recommends a strong gene flow because of wild movement of domestic *C. bactrianus*. The pronounced difference between animals and plants is their dispersal biology. In plants, the gene flow takes place through pollens and seeds, which means that the geographic system of genetic changes was generated by two different mechanisms (Hamilton & Miller, 2002; Levin, 1981; Sork, Smouse, Grivet, & Scofield, 2015). The important feature of plant dispersal is that we can notice whether genes are distributed through dispersal of seed or pollen. This distinction allows us to identify whether environmental components, i.e., phonological differences could affect differential fertilization success between populations and biotic dispersal vectors (Sork et al., 2016).

Plants have chloroplast which is haploid and non-recombinant that are important for documentation of migration, and history of population structure. Because of their uniparental inheritance, the organelle genome helps in separating the influence of two processes on phylogeography which has been studied in many tree species (Burban & Petit, 2003; Gugger, Sugita, & Cavender-Bares, 2010; Liepelt, Bialozyt, & Ziegenhagen, 2002). The important feature of plant dispersal biology is that flow of gene is leptokurtic, with most of the seeds and pollens scattering locally close to where genotypes are well adapted (Bradshaw, 1972). Trees have good

capability for long distance gene flow and large effective population sizes (Petit & Hampe, 2006). The *Pinus longaeva* of the White Mountains in California and Nevada gives a good example of the influence of longevity and large population size on phylogeography (Schierenbeck, 2014). The *Pinus longaeva* can live over 5000 years and once it was predominant at lower elevations whole of the Great Basin during the last glacial maximum. However, its present range is limited to isolated mountain tops at the western edge of its earlier distribution (Lee, Ledig, & Johnson, 2002). Because of the restricted and fragmented dispersal of *Pinus longaeva*, its level of genetic diversity is similar to that of other pines. However, we see various tree species with global distribution whose longevity may checked population contractions from resulting in complete extinction before environmental factors would allow expansion (Sork et al., 2016). Questel, Blanco-Bercial, Hopcroft, and Bucklin (2016) studied the gene movement in genus *Pseudocalanus* from Eastern North Pacific and the Pacific Arctic region. Phylogeography of *Cereoperca whiteheadi* was studied using mitochondrial *cyt b* gene and first intron of the S7 ribosomal protein gene. The results suggest that the mitochondrial *cyt b* and nuclear sequences significantly decreased the gene flow between populations *C. whiteheadi* and may be in the process of speciation (Cao, Liang, Tang, & Zhao, 2013).

3. Conclusions

The phylogeographic signature of each species is directly influenced by its surrounding environment and biotic interactions which ensconce the same and relishes its distribution. These patterns should be carefully examined and interpreted to get an idea about the changing atmospheric conditions. A lot of research needs to be undertaken for further establishment of mathematical models explaining these phylogeographic patterns.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Alley, R.B., Marotzke, J., Nordhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke, R.A., ... Wallace, J.M. (2003). Abrupt climate change. *Science*, 299, 2005–2010.
- Avise, J.C. (2000). *Phylogeography: The history and formation of species*. Cambridge, MA: Harvard University Press.
- Avise, J.C., Walker, D., & Johns, G.C. (1998). Speciation durations and Pleistocene effects on vertebrate phylogeography. *Proceedings of the Royal Society B: Biological Sciences*, 265(1407), 1707–1712.
- Bartha, L., Sramkó, G., Volkova, P.A., Surina, B., Ivanov, A.L., & Banciu, H.L. (2015). Patterns of plastid DNA differentiation in *Erythronium* (Liliaceae) are consistent with allopatric lineage divergence in Europe across longitude and latitude. *Plant Systematics and Evolution*, 301(6), 1747–1758.
- Beaumont, M.A. (2004). Recent developments in genetic data analysis: What can they tell us about human demographic history? *Heredity*, 92(5), 365–379.
- Bennett, K.D. (1983). Postglacial population expansion of forest trees in Norfolk, UK. *Nature*, 303(5913), 164–167.
- Bisconti, R., Canestrelli, D., Colangelo, P., & Nascetti, G. (2011). Multiple lines of evidence for demographic and range expansion of a temperate species (*Hylasarda*) during the last glaciation. *Molecular Ecology*, 20(24), 5313–5327.
- Bosch, F.V.D., Metz, J.A.J., & Diekmann, O. (1990). The velocity of spatial population expansion. *Journal of Mathematical Biology*, 28(5), 529–565.
- Bradshaw, A.D. (1972). Some of the evolutionary consequences of being a plant. *Evolutionary Biology*, 5, 25–47.
- Bremer, J.R.A., Viñas, J., Mejuto, J., Ely, B., & Pla, C. (2005). Comparative phylogeography of Atlantic bluefin tuna and swordfish: The combined effects of vicariance, secondary contact, introgression, and population expansion on the regional phylogenies of two highly migratory pelagic fishes. *Molecular Phylogenetics and Evolution*, 36(1), 169–187.
- Burban, C., & Petit, R.J. (2003). Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Molecular Ecology*, 12(6), 1487–1495.
- Cao, L., Liang, X.F., Tang, W., & Zhao, J. (2013). Phylogeography of *Coreoperca whiteheadi* (Perciformes: Coreoperca) in China based on mitochondrial and nuclear gene sequences. *Biochemical Systematics and Ecology*, 50, 223–231.
- Cornman, R.S., & Arnold, M.L. (2007). Phylogeography of *Iris missouriensis* (Iridaceae) based on nuclear and chloroplast markers. *Molecular Ecology*, 16(21), 4585–4598.
- Désamoré, A., Laenen, B., Devos, N., Popp, M., González-Mancebo, J.M., Carine, M.A., & Vanderpoorten, A. (2011). Out of Africa: North-westwards Pleistocene expansions of the heather *Erica arborea*. *Journal of Biogeography*, 38, 164–176.
- Dixon, C.J., Schönswetter, P., Vargas, P., Ertl, S., & Schneeweiss, G.M. (2009). Bayesian hypothesis testing supports long-distance Pleistocene migrations in a European high mountain plant (Androsace italica, Primulaceae). *Molecular Phylogenetics and Evolution*, 53, 580–591.
- Emerson, B.C. (2002). Evolution on oceanic islands: Molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology*, 11(6), 951–966.
- Escudero, M., Vargas, P., Arens, P., Ouborg, N.J., & Luceño, M. (2010). The east-west-north colonization history of the Mediterranean and Europe by the coastal plant *Carex extensa* (Cyperaceae). *Molecular Ecology*, 19, 352–370.
- Ferrera, I., Sarmiento, H., Prisco, J., Chiuchiolo, A., Gonzalez, J.M., & Grossart, H.P. (2017). Diversity and distribution of freshwater aerobic anoxygenic phototrophic bacteria across a wide latitudinal gradient. *Frontiers in Microbiology*, 8, 175.
- Francisco, S.M., Faria, C., Lengkeek, W., Vieira, M.N., Velasco, E.M., & Almada, V.C. (2011). Phylogeography of the shanny *Lipophryspholis* (Pisces: Blenniidae) in the NE Atlantic records signs of major expansion event older than the last glaciation. *Journal of Experimental Marine Biology and Ecology*, 403(1–2), 14–20.
- Françoso, E., Zuntini, A.R., Carnaval, A.C., & Arias, M.C. (2016). Comparative phylogeography in the Atlantic forest and Brazilian savannas: Pleistocene fluctuations and

- dispersal shape spatial patterns in two bumblebees. *BMC Evolutionary Biology*, 16(1), 3.
- Frederico, R.G., Farias, I.P., Araújo, M.L.G.D., Charvet-Almeida, P., & Alves-Gomes, J.A. (2012). Phylogeography and conservation genetics of the Amazonian freshwater stingray *Paratrygonaiereba* Müller & Henle, 1841 (Chondrichthyes: Potamotrygonidae). *Neotropical Ichthyology*, 10(1), 71–80.
- Gao, Y.D., Zhang, Y., Gao, X.F., & Zhu, Z.M. (2015). Pleistocene glaciations, demographic expansion and subsequent isolation promoted morphological heterogeneity: A phylogeographic study of the alpine *Rosa sericea* complex (Rosaceae). *Scientific Reports*, 5, 113. doi:10.1038/srep11698
- Gómez, A., & Lunt, D.H. (2007). Refugia within refugia: Patterns of phylogeographic concordance in the Iberian Peninsula. In S. Weiss & N. Ferrand (Eds.), *Phylogeography of Southern European Refugia* (pp. 155–188). Berlin: Springer.
- Gugger, P.F., Sugita, S., & Cavender-Bares, J. (2010). Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: Testing hypotheses from the fossil record. *Molecular Ecology*, 19(9), 1877–1897.
- Gutiérrez-Rodríguez, C., Ornelas, J.F., & Rodríguez-Gómez, F. (2011). Chloroplast DNA phylogeography of a distylous shrub (*Palicourea padifolia*, Rubiaceae) reveals past fragmentation and demographic expansion in Mexican cloud forests. *Molecular Phylogenetics and Evolution*, 61(3), 603–615.
- Hamilton, M.B., & Miller, J.R. (2002). Comparing relative rates of pollen and seed gene flow in the island model using nuclear and organelle measures of population structure. *Genetics*, 162(4), 1897–1909.
- Heuertz, M., Teufel, J., González-Martínez, S.C., Soto, A., Fady, B., Alía, R., & Vendramin, G.G. (2010). Geography determines genetic relationships between species of mountain pine (*Pinus mugo* complex) in western Europe. *Journal of Biogeography*, 37, 541–556.
- Hewitt, G.M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58(3), 247–276.
- Hewitt, G.M. (2000). The genetic legacy of Quaternary ice ages. *Nature*, 405, 907–913.
- Hickerson, M.J., Carstens, B.C., Cavender-Bares, J., Crandall, K.A., Graham, C.H., Johnson, J.B., & Yoder, A.D. (2010). Phylogeography's past, present, and future: 10 years after. *Molecular Phylogenetics and Evolution*, 54(1), 291–301.
- Hodel, R.G., de Souza Cortez, M.B., Soltis, P.S., & Soltis, D.E. (2016). Comparative phylogeography of black mangroves (*Avicennia germinans*) and red mangroves (*Rhizophora mangle*) in Florida: Testing the maritime discontinuity in coastal plants. *American Journal of Botany*, 103(4), 730–739.
- Hsü, K.J. (1972). When the Mediterranean dried up. *Scientific American*, 227, 27–36.
- Hu, Y., Qi, D., Wang, H., & Wei, F. (2010). Genetic evidence of recent population contraction in the southernmost population of giant pandas. *Genetica*, 138(11–12), 1297–1306.
- Hundertmark, K.J., Shields, G.F., Udina, I.G., Bowyer, R.T., Danilkin, A.A., & Schwartz, C.C. (2002). Mitochondrial phylogeography of moose (*Alces alces*): Late Pleistocene divergence and population expansion. *Molecular Phylogenetics and Evolution*, 22(3), 375–387.
- Jablonski, D., Huang, S., Roy, K., & Valentine, J.W. (2017). Shaping the latitudinal diversity gradient: New perspectives from a synthesis of paleobiology and biogeography. *The American Naturalist*, 189(1), 000–000.
- Jansson, R., & Dynesius, M. (2002). The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annual Review of Ecology and Systematics*, 33, 741–777.
- Kohn, L.M. (2005). Mechanisms of fungal speciation. *Annual Review of Phytopathology*, 43, 279–308.
- Krijgsman, W. (2002). The Mediterranean: Mare Nostrum of earth sciences. *Earth and Planetary Science Letters*, 205, 1–12.
- Kropf, M., Comes, H.P., & Kadereit, J.W. (2006). Long-distance dispersal vs. vicariance: The origin and genetic diversity of alpine plants in the Spanish Sierra Nevada. *New Phytologist*, 172, 169–184.
- Kropf, M., Comes, H.P., & Kadereit, J.W. (2008). Causes of the genetic architecture of south-west European high mountain disjuncts. *Plant Ecology and Diversity*, 1, 217–228.
- Kropf, M., Kadereit, J.W., & Comes, H.P. (2003). Differential cycles of range contraction and expansion in European high mountain plants during the Late Quaternary: Insights from *Pritzelago alpina* (L.) O. Kuntze (Brassicaceae). *Molecular Ecology*, 12, 931–949.
- Lai, J., Ma, J., Swigoňová, Z., Ramakrishna, W., Linton, E., Llaca, V., & Messing, J. (2004). Gene loss and movement in the Maize Genome. *Genome Research*, 14(10a), 1924–1931.
- Lee, S.W., Ledig, F.T., & Johnson, D.R. (2002). Genetic variation at allozyme and RAPD markers in *Pinus longaeva* (Pinaceae) of the White mountains. *American Journal of Botany*, 89, 566–577.
- Leite, Y.L., Costa, L.P., Loss, A.C., Rocha, R.G., Batalha-Filho, H., Bastos, A.C., & Pardini, R. (2016). Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proceedings of the National Academy of Sciences*, 113(4), 1008–1013.
- Levin, D.A. (1981). Dispersal versus gene flow in plants. *Annals of the Missouri Botanical Garden*, 233–253.
- Liepert, S., Bialozyt, R., & Ziegenhagen, B. (2002). Wind-dispersed pollen mediates postglacial gene flow among refugia. *Proceedings of the National Academy of Sciences*, 99(22), 14590–14594.
- Mansion, G., Rosenbaum, G., Schoenenberger, N., Bacchetta, G., Rosselló, J.A., & Conti, E. (2008). Phylogenetic analysis informed by geological history supports multiple, sequential invasions of the Mediterranean Basin by the angiosperm family Araceae. *Systematic Biology*, 57, 269–285.
- Martín-Bravo, S., Valcárcel, V., Vargas, P., & Luceno, M. (2010). Geographical speciation related to Pleistocene range shifts in the western Mediterranean mountains (Reseda sect. *Glaucoreseda*, Resedaceae). *Taxon*, 59, 466–482.
- Migliore, J., Baumel, A., Juin, M., & Médail, F. (2012). From Mediterranean shores to central Saharan mountains: Key phylogeographical insights from the genus *Myrtus*. *Journal of Biogeography*, 39, 942–956.
- Mila, B., Girman, D.J., Kimura, M., & Smith, T.B. (2000). Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proceedings of the Royal Society B: Biological Sciences*, 267(1447), 1033–1040.
- Ming, L., Yi, L., Sa, R., Wang, Z.X., Wang, Z., & Ji, R. (2016). Genetic diversity and phylogeographic structure of Bactrian camels shown by mitochondrial sequence variations. *Animal Genetics*, 48, 217–220. doi:10.1111/age.12511

- Mora, M.S., Lessa, E.P., Kittlein, M.J., & Vassallo, A.I. (2006). Phylogeography of the subterranean rodent *Ctenomys australis* in sand-dune habitats: Evidence of population expansion. *Journal of Mammalogy*, 87(6), 1192–1203.
- Ornelas, J.F., Sosa, V., Soltis, D.E., Daza, J.M., González, C., Soltis, P.S., & Ruiz-Sánchez, E. (2013). Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened cloud forests of Northern Mesoamerica. *PLoS One*, 8(2), e56283.
- Petit, R.J., Aguinagalde, I., de Beaulieu, J.L., Bittkau, C., Brewer, S., Cheddadi, R., & Mohanty, A. (2003). Glacial refugia: Hotspots but not melting pots of genetic diversity. *Science*, 300(5625), 1563–1565.
- Petit, R.J., & Hampe, A. (2006). Some evolutionary consequences of being a tree. *Annual Review of Ecology, Evolution, and Systematics*, 37, 187–214.
- Provan, J., & Bennett, K.D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution*, 23(10), 564–571.
- Pulido-Santacruz, P., Bornschein, M.R., Belmonte-Lopes, R., & Bonatto, S.L. (2016). Multiple evolutionary units and demographic stability during the last glacial maximum in the *Scytalopus peluncae* complex (Aves: Rhinocryptidae). *Molecular Phylogenetics and Evolution*, 102, 86–96.
- Qiu, Y.X., Fu, C.X., & Comes, H.P. (2011). Plant molecular phylogeography in China and adjacent regions: Tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. *Molecular Phylogenetics and Evolution*, 59(1), 225–244.
- Questel, J.M., Blanco-Bercial, L., Hopcroft, R.R., & Bucklin, A. (2016). Phylogeography and connectivity of the *Pseudocalanus* (Copepoda: Calanoida) species complex in the eastern North Pacific and the Pacific Arctic Region. *Journal of Plankton Research*, 38, 610–623. doi:10.1093/plankt/fbw025
- Riddle, B.R., & Hafner, D.J. (2006). Phylogeography in Historical Biogeography. In M. C. Ebach & R. S. Tangney (Eds.), *Biogeography in a changing world* (pp. 161–176). London: CRC Press.
- Rodríguez-Sánchez, F., Pérez-Barrales, R., Ojeda, F., Vargas, P., & Arroyo, J. (2008). The Strait of Gibraltar as a melting pot for plant biodiversity. *Quaternary Science Reviews*, 27, 2100–2117.
- Salvi, D., Schembri, P.J., Sciberras, A., & Harris, D.J. (2014). Evolutionary history of the Maltese wall lizard *Podarcis filfolensis*: Insights on the “Expansion–Contraction” model of Pleistocene biogeography. *Molecular Ecology*, 23(5), 1167–1187.
- Sawyer, Y.E., & Cook, J.A. (2016). Phylogeographic structure in long-tailed voles (Rodentia: Arvicolinae) belies the complex Pleistocene history of isolation, divergence, and recolonization of Northwest North America's fauna. *Ecology and Evolution*, 6, 6633–6647.
- Schierenbeck, K.A. (2014). *Phylogeography of California: An introduction*. Berkeley, CA: Univ of California Press.
- Schmitt, T. (2007). Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology*, 4(1), 11.
- Schmitt, T., & Varga, Z. (2012). Extra-Mediterranean refugia: The rule and not the exception? *Frontiers in Zoology*, 9(1), 22.
- Senczuk, G., Colangelo, P., De Simone, E., Aloise, G., & Castiglia, R. (2017). A combination of long term fragmentation and glacial persistence drove the evolutionary history of the Italian wall lizard *Podarcis siculus*. *BMC Evolutionary Biology*, 17(1), 247.
- Sork, V.L., Gugger, P.F., Chen, J.M., & Werth, S. (2016). Evolutionary lessons from California plant phylogeography. *Proceedings of the National Academy of Sciences*, 113(29), 8064–8071.
- Sork, V.L., Smouse, P.E., Grivet, D., & Scofield, D.G. (2015). Impact of asymmetric male and female gamete dispersal on allelic diversity and spatial genetic structure in valley oak (*Quercus lobata* Née). *Evolutionary Ecology*, 29(6), 927–945.
- Stewart, J.R., & Lister, A.M. (2001). Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution*, 16(11), 608–613.
- Storz, J.F., & Beaumont, M.A. (2002). Testing for genetic evidence of population expansion and contraction: an empirical analysis of microsatellite DNA variation using a hierarchical Bayesian model. *Evolution*, 56(1), 154–166.
- Suc, J.P. (1984). Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature*, 307, 429–432.
- Templeton, A.R. (2005). Haplotype trees and modern human origins. *American Journal of Physical Anthropology*, 128(S41), 33–59.
- Torroni, A., Achilli, A., Macaulay, V., Richards, M., & Bandelt, H.J. (2006). Harvesting the fruit of the human mtDNA tree. *Trends in Genetics*, 22(6), 339–345.
- Valente, L.M., & Vargas, P. (2013). Contrasting evolutionary hypotheses between two Mediterranean-climate floristic hotspots: The Cape of southern Africa and the Mediterranean Basin. *Journal of Biogeography*, 40, 2032–2046.
- Vinas, J., Bremer, J.A., & Pla, C. (2004). Phylogeography of the Atlantic bonito (*Sardasarda*) in the northern Mediterranean: The combined effects of historical vicariance, population expansion, secondary invasion, and isolation by distance. *Molecular Phylogenetics and Evolution*, 33(1), 32–42.
- Wang, H., Luo, X., Meng, S., Bei, Y., Song, T., Meng, T., & Zhang, B. (2015). The phylogeography and population demography of the Yunnan caecilian (*Ichthyophis bannanicus*): Massive rivers as barriers to gene flow. *PLoS One*, 10(4), e0125770.
- Wiantoro, S., Maryanto, I., & Abdullah, M.T. (2012). Phylogeny and phylogeography of *Myotis muricola* (Gray, 1846) (Chiroptera: Vespertilionidae) from the West and East of Wallace's Line inferred from partial mtDNA cytochrome b gene. *Pertanika Journal of Tropical Agricultural Science*, 35(2), 271–292.
- Zachos, J.C., Dickens, G.R., & Zeeb, R.E. (2008). An early Cenozoic perspective on green-house warming and carbon-cycle dynamics. *Nature*, 451, 279–283.