NRC Research Press

INTRODUCTION

The Evolution of Tree Diversity: Proceedings of the 2016 IUFRO Genomics and Forest Tree Genetics Conference, Phylogenetics and Genomic Evolution Session, Arcachon, France

Studies in the evolution of forest tree diversity face a common suite of issues: phylogenetic resolution in the context of hybridization and incomplete lineage sorting, the balance between divergence and introgression, the relative effects of local adaptation and demographic history on population genetic structure, and many others. While we know much about the impact of tree diversity on ecosystem services (Cavender-Bares 2016; Liang et al. 2016) and the assembly and maintenance of tree diversity at community and regional scales (e.g., Mason et al. 2012; Dryflor et al. 2016), we know less about the evolutionary forces shaping the origins and maintenance of tree diversity. The Phylogenetics and Genomic Evolution Session of the 2016 IUFRO Genomics and Forest Tree Genetics Conference was convened in Arcachon, France, in May 2016 (Holliday et al. 2017) to bring together researchers addressing evolutionary relationships within and among tree species. The papers in the current issue sample from the topics covered in this session and address three overarching subjects in the evolution of tree diversity.

Hybridization, the bugbear of many efforts to reconstruct the tree of life or delimit species, figures prominently in these papers. Cannon and Scher (2017) argue that in the oak syngameon (Burger 1975; Van Valen 1976), the genomic evidence of introgression so commonly reported in oaks (Zeng et al. 2011; Moran et al. 2012; Zhang et al. 2015; Sullivan et al. 2016; An et al. 2017), but often without an obvious gradient of intermediate phenotypes between parental species, is an expected outcome of their low chromosome number and conserved genome structure in conjunction with high gamete production and conspecific gamete advantage. Pham et al. (2017) revisit classic work on the geographic structure of chloroplast variation in the white oak group (Whittemore and Schaal 1991; Dumolin-Lapègue et al. 1997; Petit et al. 1997) using whole plastome sequencing in combination with restriction-site associated DNA sequencing (RAD-seq) of the nuclear genome. They find that the geographic structure of the plastome we might expect in the eastern North American white oak syngameon (cf. Hardin 1975) is lacking: phylogenetic informativeness of the plastome attenuates towards the tips of the white oaks, but it is not associated, at least in eastern North America, with strong phylogeographic signal. McVay et al. (2017*a*) provide genomic evidence of historic introgression between a lobed white oak of eastern North America and two lobed white oaks of western North America that are no longer sympatric, resolving in the process an old phylogenetic puzzle: the placement of *Quercus gambelii*. The methods they use to tease apart the signal of ancient hybridization from that of population divergence in reduced-representation sequencing data augments the analytical toolkit for reconstructing the tree of life in hybridizing lineages.

Phylogenetic inference is often problematic in trees, particularly oaks (Hipp 2015; Eaton et al. 2015; Hu et al. 2016; McVay et al. 2017*b*), where ongoing hybridization, high heterozygosity, and incomplete lineage sorting all present challenges. Four papers in this volume use genomic approaches to investigate phylogenetic relationships in a genus or family. Two discussed above (McVay et al. 2017*a*; Pham et al. 2017) utilize the RAD-seq method to reconstruct phylogenetic relationships in the white oaks. RAD-seq, however, is still somewhat in its infancy for phylogenetics, and analytical approaches are not fully agreed upon (Ree and Hipp 2015). Fitz-Gibbon et al. (2017) address one of the analytical questions that lingers with short-read, anonymous RAD-seq data: is it preferable to map data back to a reference genome to identify sequence regions for analysis? or is de novo clustering (using, e.g., PyRAD) (Eaton 2014) equally effective? They demonstrate that, at least in their study, these alternative approaches recover congruent phylogenies with approximately the same levels of support, providing at the same time insights into the phylogeny of the California white oaks. Kua and Cannon (2017) take a slightly different approach to phylogenetic inference in their study, using a reference-free comparative analysis of genome skimming data in *Ficus* and *Lithocarpus* against the context of life history differences; they estimate the effect of hybridization on genealogical concordance across the genome. Their work demonstrates that our expectation of high rates of hybridization in the large-seeded, wind-pollinated *Lithocarpus* is supported by higher among-species genome sharing and genomic heterogeneity of the phylogenetic signal.

The last three papers in this issue address the evolution of genetic diversity within species, both in selected genes (Meireles et al. 2017) and at neutral loci (Costa et al. 2017; Merceron et al. 2017). Meireles et al. demonstrate patterns of natural selection on two cold response candidate genes, using population genetic approaches to investigate selection within species, and phylogenetic approaches to investigate selection during the course of diversification of the approximate six species of *Quercus* section *Virentes*. The authors demonstrate that a legacy of cold acclimation ability in the northern temperate ancestors of this clade proved adaptive as the *Virentes* migrated into the tropics, as populations of a single species in the clade may encounter very different conditions of winter cold across wide latitudinal distributions. Costa et al. revisit the population genetic structure of *Eucalyptus globulus* to identify the source of Portuguese introductions as southern and eastern Tasmania, demonstrating that the Portuguese landrace has remarkably high diversity relative to the species as a whole. Finally, Merceron et al. undertake a rangewide investigation of population genetic structure in northern red oak (*Quercus rubra*), sampling populations from throughout its native range in eastern North America and 38 populations from its introduced range in Europe. They partition the continuous variation in North America using a combination of clustering, AMOVA, and approximate Bayesian computation to test alternative models of population genetic divergence, concluding that European introductions likely find their source in northeastern North America and that the continuous variation observed in North America is due at least in part to secondary contact between predominantly allopatric northern and southern populations.

A motif woven through most of these papers—and indeed, through the conference as a whole (Holliday et al. 2017)—is the importance of genome-scale data and explicit model-based hypothesis testing to addressing even basic questions in the evolution of tree diversity. Analyses based on a handful of loci and summary statistics will probably always play an important role in rangewide surveys of genetic diversity, identification of hybrid individuals, broad-scale or initial phylogenetic surveys, and the characterization of phylogenetic and genetic diversity of communities. But the work presented here demonstrates the power of integrating

Published by NRC Research Press

high-throughput sequencing data with hypothesis-driven model-testing approaches to infer the complex and interacting forces that shape biodiversity evolution. This integration is becoming the standard across biodiversity science, and we look forward to seeing how our insights into the origins of tree diversity evolve in the years to come.

Acknowledgements

Thanks to Christophe Plomion, chair of the conference organizing committee; the co-chairs of the organizing and scientific communities; the speakers who made this conference a success; and Chuck Cannon for thoughts on a first draft of this introduction.

References

An, M., Deng, M., Zheng, S.-S., Jiang, X.-L., and Song, Y.-G. 2017. Introgression threatens the genetic diversity of *Quercus austrocochinchinensis* (Fagaceae), an endangered oak: a case inferred by molecular markers. Front. Plant Sci. **8**: 229. PMID:28270827.

Burger, W.C. 1975. The species concept in *Quercus*. Taxon, **24**(1): 45–50. doi:10.2307/1218998.

Cannon, C.H., and Scher, C.L. 2017. Exploring the potential of gametic reconstruction of parental genotypes by F_1 hybrids as a bridge for rapid introgression. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0181. PMID:28732173.

Cavender-Bares, J. 2016. Diversity, distribution, and ecosystem services of the North American oaks. International Oaks, **27**: 37–48.

Costa, J., Vaillancourt, R.E., Steane, D.A., Jones, R.C., and Marques, C. 2017. Microsatellite analysis of population structure in *Eucalyptus globulus*. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0218. PMID:28679070.

Dryflor, Banda-R, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., et al. 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science, **353**(6306): 1383–1387. doi:10.1126/science.aaf5080. PMID:27708031.

Dumolin-Lapègue, S., Demesure, B., Fineschi, S., Le Corre, V., and Petit, R.J. 1997. Phylogeographic structure of white oaks throughout the European continent. Genetics, **146**(4): 1475–1487. PMID:9258689.

Eaton, D.A.R. 2014. PyRAD: assembly of de novo RADseq loci for phylogenetic analyses. Bioinformatics, **30**(13): 1844–1849. doi:10.1093/bioinformatics/btu121. PMID:24603985.

Eaton, D.A.R., Hipp, A.L., González-Rodríguez, A., and Cavender-Bares, J. 2015. Historical introgression among the American live oaks and the comparative nature of tests for introgression. Evolution, **69**(10): 2587–2601. doi:10.1111/evo.12758. PMID:26299374.

Fitz-Gibbon, S., Hipp, A.L., Pham, K.K., Manos, P.S., and Sork, V.L. 2017. Phylogenomic inferences from reference-mapped and de novo assembled short-read sequence data using RADseq sequencing of California white oaks (*Quercus* section *Quercus*). Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0202.

Hardin, J.W. 1975. Hybridization and introgression in *Quercus alba*. J. Arnold Arbor. **56**(3): 336–363.

Hipp, A.L. 2015. Should hybridization make us skeptical of the oak phylogeny? International Oaks, **26**: 9–18.

Holliday, J.A., Aitken, S.N., Cooke, J.E.K., Fady, B., González-Martínez, S.C., Heuertz, M., et al. 2017. Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding. Mol. Ecol. **26**(3): 706–717. doi:10.1111/mec.13963. PMID:27997049.

Hu, Y., Woeste, K.E., and Zhao, P. 2016. Completion of the chloroplast genomes of five Chinese *Juglans* and their contribution to chloroplast phylogeny. Front. Plant Sci. **7**: 1955. PMID:28111577.

Kua, C.-S., and Cannon, C.H. 2017. Patterns of genomic diversification reflect differences in life history and reproductive biology between figs (*Ficus*) and the stone oaks (*Lithocarpus*). Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0188. PMID:28472589.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al. 2016. Positive biodiversity–productivity relationship predominant in global forests. Science, **354**(6309). doi:10.1126/science.aaf8957.

Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A., and Allen, R.B. 2012. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. J. Ecol. **100**(3): 678–689. doi:10.1111/j.1365-2745.2012.01965.x.

McVay, J.D., Hauser, D., Hipp, A.L., and Manos, P.S. 2017*a*. Phylogenomics reveals a complex evolutionary history of lobed-leaf white oaks in western North America. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0206. PMID:28727934.

McVay, J.D., Hipp, A.L., and Manos, P.S. 2017*b*. A genetic legacy of introgression confounds phylogeny and biogeography in oaks. Proc. R. Soc. B Biol. Sci. **284**(1854): 20170300. doi:10.1098/rspb.2017.0300.

Meireles, J.E., Beulke, A., Borkowski, D.S., Romero-Severson, J., and Cavender-Bares, J. 2017. Balancing selection maintains diversity in a cold tolerance gene in broadly distributed live oaks. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0208. PMID:28683204.

Merceron, N.R., Leroy, T., Chancerel, E., Romero-Severson, J., Borkowski, D.S., Ducousso, A., et al. 2017. Back to America: tracking the origin of European introduced populations of *Quercus rubra* L. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0187. PMID:28750176.

Moran, E.V., Willis, J., and Clark, J.S. 2012. Genetic evidence for hybridization in red oaks (*Quercus* sect. *Lobatae*, Fagaceae). Am. J. Bot. **99**(1): 92–100. doi:10.3732/ajb.1100023. PMID:22174334.

Petit, R.J., Pineau, E., Demesure, B., Bacilieri, R., Ducousso, A., and Kremer, A. 1997. Chloroplast DNA footprints of postglacial recolonization by oaks. Proc. Natl. Acad. Sci. U.S.A. **94**(18): 9996–10001. doi:10.1073/pnas.94.18.9996. PMID:11038572.

Pham, K.K., Hipp, A.L., Manos, P.S., and Cronn, R.C. 2017. A time and a place for everything: phylogenetic history and geography as joint predictors of oak plastome phylogeny. Genome, **60**(9). [This issue.] doi:10.1139/gen-2016-0191. PMID:28445658.

Ree, R.H., and Hipp, A.L. 2015. Inferring phylogenetic history from restriction site associated DNA (RADseq). *In* Next-generation sequencing in plant systematics. *Edited by* E. Hörandl and M. Appelhans. Koeltz Scientific Books, Koenigstein. pp. 181–204.

Sullivan, A.R., Owusu, S.A., Weber, J.A., Hipp, A.L., and Gailing, O. 2016. Hybridization and divergence in multi-species oak (*Quercus*) communities. Bot. J. Linn. Soc. **181**(1): 99–114. doi:10.1111/boj.12393.

Van Valen, L. 1976. Ecological species, multispecies, and oaks. Taxon, **25**(2–3): 233–239. doi:10.2307/1219444.

Whittemore, A.T., and Schaal, B.A. 1991. Interspecific gene flow in sympatric oaks. Proc. Natl. Acad. Sci. U.S.A. **88**(6): 2540–2544. doi:10.1073/pnas.88.6.2540. PMID:11607170.

Zeng, Y.-F., Liao, W.-J., Petit, R.J., and Zhang, D.-Y. 2011. Geographic variation in the structure of oak hybrid zones provides insights into the dynamics of speciation. Mol. Ecol. **20**(23): 4995–5011. doi:10.1111/j.1365-294X.2011.05354.x. PMID:22059561.

Zhang, R., Hipp, A.L., and Gailing, O. 2015. Sharing of chloroplast haplotypes among red oak species suggests interspecific gene flow between neighboring populations. Botany, **93**(10): 691–700. doi:10.1139/cjb-2014-0261.

Andrew L. Hipp
The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532-1293, USA;
The Field Museum, 1400 S Lake Shore Drive, Chicago, IL 60605, USA.

Santiago C. Gonzalez-Martinez
BIOGECO (Biodiversité Gènes et Communautés), INRA, Univ. Bordeaux,
69 route d'Arcachon, Cestas, France.

Juan P. Jaramillo-Correa
Department of Evolutionary Ecology, Institute of Ecology, Universidad
Nacional Autónoma de México, AP 70-275, Mexico City, CDMX 04510,
Mexico.