

## Meetings

# Gaining a global perspective on Fagaceae genomic diversification and adaptation

**IUFRO 'Genetics and genomics of Fagaceae and Nothofagaceae' Conference, Shanghai Chenshan Botanical Garden, China, November 2017**

### Introduction

The family Fagaceae is one of the most comprehensively studied and species rich groups of trees in the world. It provides a powerful model lineage for the general advance of tree science (Petit *et al.*, 2013) and contributes enormously to global ecosystem services (Cavender-Bares, 2016). Biodiversity hotspots for Fagaceae are found in both temperate and tropical forests – which is unusual among trees – where they have undergone numerous independent and parallel diversifications (Kremer *et al.*, 2012). Major genera provide possibilities for comparative studies within and across biomes and life histories, such as modes of pollination. Northern temperate groups including oak (*Quercus*) and beech (*Fagus*) are deciduous and wind-pollinated, and produce simple nuts exemplified by the classic oak acorn. In terms of biomass, these trees often dominate the forests in which they are found. These temperate groups are the best studied in the family while not being representative of Fagaceae biology. By contrast, the subtropical and tropical groups, primarily stone oaks (*Lithocarpus*) and tropical chestnuts (*Castanopsis*), are insect-pollinated and produce a variety of nut types. They are scattered across mega-diverse forests, contributing only a small proportion to overall biomass. By expanding our studies of Fagaceae trees to include the entire diversity across the family, we would create a powerful comparative framework for the study of tree adaptation and response to global environmental changes (Table 1).

Because of their evolutionary characteristics, the family also provides a good model for comparative biogeography (Petit *et al.*, 2002; Chen *et al.*, 2012). While glacial periods restricted European and North American oaks to refugia, glacial periods had little impact on Mexican oaks (González-Rodríguez *et al.*, 2004), Californian oaks (Grivet *et al.*, 2006; Gugger *et al.*, 2013), and Southeast Asian stone oaks (Cannon & Manos, 2003). Additionally, frequent hybridization and genetic introgression among species leads to shorter coalescent times within communities, reinforcing biogeographical patterns. These characteristics allow a detailed study of the impact of past climate changes on the patterns of genetic diversification and adaptation found within each group, across several biomes. Given that we cannot understand the future

of forests without understanding their past (Petit *et al.*, 2008), a global comparative study of Fagaceae would allow simultaneous interpretations of major shifts across biomes with contrasting responses to glacial-driven changes.

### IUFRO 'Genetics and genomics of Fagaceae and Nothofagaceae' conference 2017

The special IUFRO (<http://www.iufro.org/>) working group meeting held at the Shanghai Chenshan Botanical Garden, China, collated recent advances in research and the people needed to build this global perspective. Convened in November 2017, the meeting brought together over 60 scientists from 15 countries covering the biogeographic, taxonomic and phenotypic range of the family. Attendees discussed strategies for effective future collaboration, capitalizing on current results. While most genomic resources originate with temperate groups, conserved genome structure will facilitate their application to tropical groups (Plomion *et al.*, 2016).

The valley oak (*Quercus lobata*) of California is the newest available genome assembly. Victoria Sork presented her research team's work (Steve Salzberg, Sorel Fitz-Gibbon, Daniela Puiu, Matteo Pellegrini and Aleksey Zimin) showing the great benefit of validation against the assemblies of pedunculate oak (*Quercus robur*) and utilizing recent technical advances, such as Pac-Bio/Illumina hybrid sequencing and Dovetail Genomics. Likewise, John Carlson detailed how the assembly of the Chinese chestnut (*Castanea mollissima*) genome, based upon earlier genome sequencing technologies, has continued to improve through reference to the *Quercus* genome assemblies.

Given these genomic resources and the comparative framework offered by the diversity found in the Fagaceae, we can unlock some of the mysteries of how trees have been so successful over tens of millions of years (Petit & Hampe, 2006). For example, detailed analyses of the pedunculate oak genome have produced profound insights into how trees may adapt to the continual fluctuation of their biotic and abiotic environments over their long lifespan. As shown by Christophe Plomion, the diverse molecular arsenal of defence weapons (immune receptors) against pathogens is probably a key element of their longevity. Abundant evidence also indicates that tree species do not evolve in isolation but as members of a syngameon, as suggested by Chuck Cannon. Oliver Gailing reported that observed gene flow among North American red oak species is related to adaptation for drought tolerance. An RAD-seq analysis by Ye Sun, of 42 Chinese *Castanopsis* species, suggests a complicated evolutionary history, implicating hybridization as a creative rather than destructive force. Based on experiments using sympatric white oak species, Warren Chatwin and Jeanne Romero-Severson demonstrated strong support for the Local Gene Pool hypothesis, in which hybrid offspring suffer lower mortality than pure offspring, due presumably to adaptive gene

**Table 1** Characteristics of major groups in family Fagaceae

Genus	Biomes	Continents	No. of species	Pollination	Fruit type
<i>Fagus</i>	Temperate; deciduous	North America, Europe, Asia	11	Wind	Angular trigonous nut, splitting capsule
<i>Trigonobalanus</i>	Tropical; evergreen	Hainan Island, Indochina, Peninsular Malaysia, North Borneo, Colombia	3	Inconclusive, insect probable	Angular trigonous nut, splitting capsule
<i>Chrysolepis</i>	Temperate; evergreen	Pacific Northwest	2	Generalized insect	Angular trigonous nut, splitting capsule
<i>Lithocarpus</i>	Tropical, subtropical; evergreen	Assam, Indochina, Southeast Asia to Papua	c. 300	Generalized insect	Round nut, valveless cupule; acorn and enclosed receptacle
<i>Castanopsis</i>	Tropical, subtropical; evergreen	Assam, Indochina, Southeast Asia to Papua	c. 150	Generalized insect	Rounded trigonous nut, splitting capsule
<i>Castanea</i>	Subtropical, temperate; deciduous	Europe, North America, Asia	12	Generalized insect	Rounded trigonous nut, splitting capsule
<i>Notholithocarpus</i>	Temperate; evergreen	North America (limited to Pacific Northwest)	1	Generalized insect	Round nut, valveless cupule; acorn
<i>Quercus</i>	Temperate, subtropical, tropical; evergreen, deciduous	North America, Europe, Asia	c. 435	Wind	Round nut, valveless cupule; acorn

Trees; northern hemisphere origins and distribution; incomplete reproductive isolation barriers; haploid chromosome number = 12; limited evidence of whole genome duplication; predominantly hypogeal germination.

flow among species. Yet adaptive gene flow is not rampant: Victoria Sork presented data demonstrating limits to introgression and hybridization, which probably occurs only under special circumstances. Chai-Shian Kua presented results from a comparative genomic analysis of stone oaks (*Lithocarpus*) and figs (*Ficus*) which demonstrate that genomic divergence is highly affected by life history strategy (Kua & Cannon, 2017). We should expect such special circumstances to become all too common in the Anthropocene.

### Three dimensions of evolution (environment–phenotype–genotype)

The direct study of genomic sequence and structure requires a detailed and complementary understanding of phenotypic variation and its genetic and environmental determinants. Lack of high-throughput and standardized phenotyping has become the limiting factor to our understanding of adaptation. We need high resolution data, both temporally and spatially, of all three elements of evolution in these trees: genomic sequence and structure, phenotypic responses, and environmental variation.

Gregoire Le Provost demonstrated that gene expression, the most fundamental level of phenotype, plays a big role in ecological preferences and shaping adaptive phenotypes of species, particularly between *Q. robur* and *Quercus petraea*. His work on waterlogging and drought stress demonstrated the centrality of the suberin, ethylene and fermentation pathways to successful adaptation. Advances in mass-spectrometric methods allowed Benjamin Brachi to study 130 secondary metabolites in 1800 trees of both species, revealing that most variation is found within, rather than among, populations. Carbon isotopes, a time-tested approach for the measurement of water use efficiency in leaves, were applied to interspecific crosses to study the genetics of water use efficiency in pure species and hybrid individuals in a common garden setting. On a macro-phenotyping scale, Jialin Song utilized X-ray based

tomography to screen whole trunks for underlying internal structures of branching traits, providing important genetic information on growth form and wood quality. At a community level, Fang K. Du's study suggested that above- and belowground diversification, in trees and their microbial communities, exhibits correlated responses to deep environmental change in *Quercus aquifolioides*.

This triangulation among the three major dimensions of understanding tree diversification and adaptation can benefit greatly from the use of common gardens, particularly distributed networks of plantings, as demonstrated by Charalambos Neophytou. This approach will improve our understanding of adaptation, notably in the context of climate and ecosystem change, and a compilation of existing experimental resources is much needed. Adding another super-imposed dimension, Victoria Sork also presented exciting work on the possible impact of epigenetic imprinting, providing another possible avenue through which trees may gain a 'shortcut' in adapting to local conditions and allowing an additional evolutionary flexibility beyond a slow selection process through the accumulation of adaptive mutations.

The meeting highlighted the need for comparative studies across continents and clades, using common genomic markers and analytical methods. Two comparable phylogenetic studies based on restriction site associated DNA (RAD-seq) highlighted the insights that can be gained. In the oaks of *Quercus* sect. *Cyclobalanopsis*, the cycle cup oaks were shown to be an ancient lineage along the Tethyan Sea that diversified following the uplift of the Himalayas and resulting climatic perturbations (Deng *et al.*, 2018). Meanwhile, during the initial diversification of sect. *Cyclobalanopsis*, the two major oak clades of the Americas (sects. *Lobatae* and *Quercus*) were diversifying simultaneously and in parallel (Hipp *et al.*, 2018). North American red and white oaks co-diversified along the east and west coasts and then each merged into new Mexican lineages between 10 and 20 million years ago. This parallel history – as

temperate zones expanded and tropical tree species were pushed south – most likely explains the high diversity of oaks in the Americas (McVay *et al.*, 2017). Comparing these patterns across clades (red oaks, white oaks, ring-cupped oaks) and continents (North America, East Asia) provides us with the opportunity to understand the determinants of woody plant diversity and extend this work into Mexico. An ongoing collaboration among scientists from Mexico and other countries is investigating why oak diversification increased in the tropics.

Additionally, with increasingly sensitive analyses, we are now gaining a glimpse into more recent changes. Due to their very large genetic diversity, oaks might indeed undergo evolutionary changes over a limited number of generations as a response to strong selective factors. Antoine Kremer showed how genetic changes during the Holocene can be tracked by the retrieval of ancient DNA from fossil or archeological remains at different time scales (Wagner *et al.*, 2018). Allochronic approaches thus complement traditional synchronic surveys of genetic diversity to retrace recent evolutionary trajectories.

## The Fagaceae in the Anthropocene

Given its complex evolutionary history and keystone ecological role, how will the Fagaceae fare in the future as humans modify the Earth's environment to serve their purposes? One apparent weakness that emerged is the lack of conservation genetics at comparable genomic and geographical scales to evolutionary and ecological studies. Murphy Westwood detailed current efforts to assess the scale of wild genetic diversity captured in *ex-situ* collections. However, participants noted that the lack of common markers and affordable genotyping toolkits limits the incorporation of genomic tools into current conservation efforts.

Because environmental change during the Anthropocene is expected to accelerate, the balance among the three evolutionary dimensions should also be expected to change. For current levels of Fagaceae diversity to be maintained, the discovery of feasible ways of managing and conserving trees in this family must likewise be accelerated. An ongoing discussion throughout the conference addressing these challenges led to a call for the use of common tools (genetic markers, phenotypic measurements), and shared approaches and materials (common gardens and tissues). Mutually agreed-upon protocols and analyses could greatly facilitate global discovery.

Ultimately, the hotspots of diversity have not been hotspots of research. This meeting represents a changing tide, due largely to increasing participation from colleagues in Asia and the translation of technological and analytical advances from other organisms. Elements missing from the meeting included the other major diversity hotspot in Mexico and much of Southeast Asia. In preparation for the next meeting of this group, a plan has been created to establish the conditions necessary to truly gain a global perspective on the Fagaceae.

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