International Oaks

The Journal of the International Oak Society

Proceedings

9th International Oak Society Conference
October 21-24, 2018

Issue No. 30 / 2019 / ISSN 1941-2061

This issue is dedicated to Michael Avishai, Bob Berry, and Doug McCreary each of whom has inspired oak enthusiasts around the world. May their memory live on in the oak trees that we grow and in the understanding we come to have of them.

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International Oak Society Officers and Board of Directors 2018-2021

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Cover illustration: Lisa Fowler (California scrub-jay); courtesy of Tim Vendlinski.
Photos. Page 10: Guy Sternberg. Page 11: Cécile Souquet-Basiège. Page 13: Andrew Hipp.

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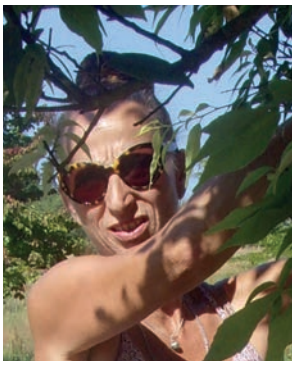

INTRODUCTION

Of Oaks and Men[1]

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California is a great many things for me, and to these must now be added the 9th International Oak Society Conference that these Proceedings represent. This Conference was our most ambitious to date and we are indebted to the entire crew responsible for its success, with special thanks to Emily Griswold who accepted the challenge of leading its organization, and who has written the Preface to this volume. We were, as I have heard since the end of the Conference from several of the authors of these pages, very lucky: only days after the end of our event, the alarming air quality in Davis from smoke from nearby wildland fires resulted in school closings and injunctions from local authorities to stay at home, where those inhabitants who could afford to do so have installed air filtering systems. Analysts of the world's seventh most important economy report that air filtering is now a booming business in California.

Photo 1/ *Aphelocoma californica,* one of the many birds of California whose lives are intimately intertwined with the genus *Quercus*.

My years as a bird-watcher took me on four fantastic California road trips from north to south, zigzagging from east to west, tracking with heavy and cumbersome telephoto lenses the vibrant colors and exuberant life of the unique – as so

1. It will be understood that this is a literary, not a sexist, reference.

many things are in California – avifauna. It is always with great fondness and a bit of nostalgia that I read about the love affairs between birds and oaks such as described in this volume by Airola and Greco. Since my own love affair with the genus *Quercus* began, the same foundness infuses my reading about similar ties between oaks and other inhabitants of the planet, including *Homo sapiens*.

In these pages Pearse reviews the complex interactions between insect herbivores and our favorite trees, stressing the fact that creating habitat for these creatures could be a great benefit of planting native oaks. On the human side, those of you who attended the 8th International Oak Society Conference at The Morton may remember my infatuation with the history of acorn consumption in the biological and social evolution of mankind. Brand and Lake each take this into the present with their work in promoting the study and conservation, for the former, of *Quercus rotundifolia* in the *dehesas* of the Iberian Peninsula and, for the latter, of *Notholithocarpus densiflorus*, for its importance in native American culture. Taylor tells the story of a unique episode in the history of *Q. suber* in the United States during which millions of these trees were planted across the country, while Sanchez and Wyly describe a unique program intended to engage students in the preservation and growth of native trees in California's urban forests. Because 55% of the world's population currently lives in urban areas – and this is expected to rise to 70% by 2050 – the value of urban forest is undeniable. Lamant tells us of the interest and obstacles in France for urban oak plantings and Denig outlines general considerations for planting oaks in urban landscapes of the future. Spotswood et al. review the history and evolution of the landscape in the part of California known today as Silicon Valley, arguing that reintroduction of native oaks could help to increase the ecological functions of the urban forest.

Of course, the love affair between humans and oaks, as well as the desire to plant these trees, is not limited to those striving to improve the urban environment. Muick paints a brief introduction to the oaks of California, focusing on eight species, while Baldwin, Giseburt, Haddock, and Lobdell, in their respective reports of the Pre- and Post-Conference Tours, illustrate most vividly the human passion and interest that these trees and their ecosystems nourish. Weathington shares with us observations gleaned over the past 40 years on the performance of several Asian evergreen oaks (section *Cyclobalanopsis*) at the JC Raulston Arboretum in Raleigh, North Carolina and Krautmann tells of concerted efforts to propagate and diffuse interesting cultivars of Southwestern U.S. oaks, while Russell and Jablonski review the new cultivars from all over the world available in the trade since 2015. Barnea recounts the history of the demise of the *Q. ithaburensis* forests that once covered vast areas in what is present-day Israel and his – and others' – efforts to remedy, if only in part, this situation.

Photo 2/ Pre- and Post-Conference Tour participants enjoyed the oak diversity of California, including the marvelous *Quercus chrysolepis*.

Enlarging our horizons, Cannon tells of his fascination with one of the other genera in the Fagaceae, *Lithocarpus*, and reviews the major Asian lineages of the family. He reminds us that everything that makes an acorn is not necessarily an oak and describes the (some resolved, some unresolved) relationships, both ecologic and genetic, that structure the family and its history.

When my passion for oaks eclipsed my obsession with birds, California remained an important destination. Three fantastic voyages, with a much lighter and not-at-all-cumbersome digital camera, saw me again in California tracking the members of the family Fagaceae that grace with their presence the Golden State. And long, long before my bird and oak passions, there was Jack. Born in San Francisco, Jack London's last dwelling can be visited in the Jack London State Historic Park, part of a grouping of California State Parks that includes Sugarloaf Ridge State Park, the first stop of the second Pre-Conference Tour. Until the end of the 20th century this Park was a mecca for bird watchers: a symphony orchestra would have been shamed to silence by the extraordinary music of the countless bird songs that could be heard. In 2004, the choir of birds was reduced to a solo.

I am sad about this.

We should all be sad about this.

As sad as John Steinbeck was angry when he wrote in *The Grapes of Wrath* (1939), "There is a crime here that goes beyond denunciation." Of course, he wasn't writing about air or oaks or birds. He was writing – 80 years ago – about the devastating effects, on many levels, of California's agricultural industry.

Many in these pages write about the historical and present-day modifications to the natural landscape in California and the significance of this in the context of the Anthropocene and its already-evident consequences such as the extreme fire events that have plagued California for a number of years now as well as the ever-growing number of new pathogen and pest behaviors that indicate that they too are adapting to survive in a modified environment.

Ackerley et al. tell of the dramatic 2017 Tubbs Fire, that burned 14,895 hectares, and the ensuing study to provide a baseline for examining potential vegetation changes after such high-severity fires. The Tubbs Fire is also the subject of Halbur et al. in the context of predictions of increased fire frequency in the North Coast region of California; the authors stress that long-term monitoring of wildfire in the region is important to increase knowledge about oak-forest resiliency. Koenig reviews changes in acorn production over the past 30 years, remarking that while climate change has played a role, the most dramatic effects on oak populations are due to land-use changes. Dagit reviews drought and beetle impacts to native trees at the urban/wildlife interface in the Santa Monica Mountains since 2014 and the initiatives taken to develop management strategies to meet projected future challenges. Burke sketches for us the ambitious 75-year UC Davis Living Landscape Adaptation Plan, and Moskow describes efforts by the California Oaks program to use the state's climate laws to protect oaks given that state-wide legislation for protecting trees is limited.

California is of course not the only place on the planet where the effects of the Anthropocene are being felt. Kopler and Bar-Shalom discuss oak decline and mortality of oaks in the Golan Heights and their research to characterize the health status of these following several periods of severe summer drought. Williams et al. discuss the impacts of climate change on the oaks of Oaxaca (Mexico), concentrating on the two principal

Photo 3/ Increased collecting efforts all over the world are essential for developing sound conservation strategies.

vegetation types found there: oak forest and mixed conifer-oak forest. The good news is that a consensus model shows that the center and inland parts of Oaxaca (where these vegetation types are dominant) are among those expected to be the least in danger from climate change – but the authors underline the fact that habitat degradation and forest-loss are equally important threats. Muzika and Morin examine oak mortality and decline in the Midwestern U.S. in correlation with abiotic and biotic factors to better understand patterns of forest evolution. Concern about the status of *Q. arbutifolia*, a rare Asian oak, has motivated Li et al. to develop improved micropropagation techniques, while Denvir et al. describe an ensemble of conservation strategies being deployed in Latin America, pointing out that various tools to prevent extinctions already exist, but that they are not always used. Coombes et al. tell of their intensive fieldwork in Puebla (Mexico) to find unreported species and better understand species distributions, highlighting the fact that without this basic knowledge, conservation efforts are handicapped. Correa, reviews the past ten year's worth of contributions to oak genetics and conservation in Mexico and the Neotropics, what is known about their diversity and the threats that they face. Boland discusses the value of ArcGIS technologies to scientists, land-planners and conservationists in an example that takes us to Martha's Vineyard (Massachusetts; U.S.A.) while Cameron and Coombes, on one hand, and Lobdell, on another, write of two examples that illustrate at once the importance of ex-situ oak collections and of pooling resources: the Cultivated Oaks of the World project, and the Plant Collections Network Multisite *Quercus* Collection, respectively.

Lee et al. focus their attention on *Phytophthora ramorum*, noting that although scholars have learned much in the recent past about this pathogen, our understanding of its potential to alter landscapes is only just beginning. Sternberg details a complex procedure for dealing with trees in a collection infected with oak wilt disease, possibly the most serious of all modern oak ailments, and Denman et al., focusing on acute oak decline, have developed a new, holistic approach to getting a grasp on polymicrobial interactions and disease expression.

Since it appears that putting an end to the activities that have created this havoc is, sadly, not seriously on the world's agenda, it is laudatory that so many attempts to foresee what the future holds are. But is that the only reason? Is there not also simply an

expression here of what is truly unique to our species, that is, the ability to ask questions, to interrogate the world at large, to have an opinion, to tell a story, in short, to understand? This is, I think, what Charles Darwin meant when he criticized the position held by others of his time that science is merely about collecting facts (Darwin 1861). In this volume, there are brilliant examples of this quest to understand what is *Quercus*, and, implicitly, what is this extraordinary thing called life.

One hundred and sixty years after the publication of *The Origin of Species*, the ideas expressed in these pages by Hipp et al. are as exciting as they are proof of the pertinence of Darwin's criticism. There is not one but many stories embedded in a genome. That the most interesting story may be the one told by the sutures between the genes, the changes from one story to another, and that quite possibly the "genes that distinguish *Q. macrocarpa* from *Q. bicolor* in Wisconsin are not the genes that distinguish it from *Q. stellata* in Missouri." Delving into this question, Garner et al. provide previously undemonstrated evidence for genetic differentiation within a species: two genotypes for *Q. macrocarpa* "that separate from each other more readily in admixture analysis than *Q. macrocarpa* does from *Q. bicolor*." As Hipp et al. write, we are perhaps close to being able "to ask two previously unanswerable questions: what do we mean by "species" and "phylogenies" when we are talking about oaks?"

After Denk et al. (2017) the major challenges in understanding the genus *Quercus* at infrasectional level lie, on one hand, in resolving the incongruence between traditional (morphological) and DNA-based classification systems, and, on the other, in refining our understanding of the biogeographical and ecological context of the infrasectional evolutionary history of the genus.

Keuter and Manos report here on a remarkable study, an exemplary collaboration between academic and citizen science, and a step towards resolving the incongruence mentioned above using data generated from morphology and genetics to paint a clearer picture of the relationships among the California Red Oaks (*Agrifoliae*), while raising some new and interesting questions. Perhaps also, this study points to a weak spot of historical morphology-based classification systems: the quantity of data used to determine where to put what. A lesson to be learned for those of us who often lend unwarranted significance to a very minute sample of observed morphological variation: in this study, 18,000 morphological measurements were taken.[2]

Dodd and Papper, focusing also on the California Red Oaks, report similar findings for the confirmation of the identification of the four named species in the clade, and express similar doubts concerning the named varieties of *Q. parvula*. Long et al. look at a mysterious hybrid on Santa Cruz Island, long thought to be *Q.* ×*morehus*, though neither of the parent species (*Q. kelloggii* and *Q. wislizeni*) is present on the Island. Nuclear and chloroplast DNA microsatellite results suggest that this may in fact be a hybrid between the former and *Q. agrifolia* (*Q.* ×*chasei*); several hypotheses are proposed as to how *Q. kelloggii* got involved.

Papper addresses here the interesting question of species integrity and the maintenance of reproductive compatibility within sections of the genus *Quercus* despite a long history of divergence. Focusing on the distribution of two White Oak species, *Q. douglasii* and

2. Darwin, despairing as he was over "the utter confusion my poor dear Barnacles are in," spent eight years of his life measuring thousands of barnacles that he received from correspondents all over the world, in addition to the ones he collected himself, before proposing a classification for the Cirripedia (Burkhardt 1996; letter to J.S. Henslow, July 2, 1848). It is also interesting to note that just about up until Darwin's time (nearly) everybody, including himself, who was engaged in what we would call "science" but what was called at the time "natural history" or "natural philosophy" was …a citizen scientist.

Photo 4/ In the incredible diversity in the *Quercus* world, what allows different species to remain distinct in the face of regular gene flow? Are species differentiated by adaptation to different habitats in the environment? What is the role of epigenetic mechanisms? And what of the stories told by the different sutures between the genes? These are some of the questions that we look forward to hearing more about in Taiwan in 2021. (a) *Q. robusta* (b) *Q. albocincta* (c) *Q. gravesii* (d) *Q. kelloggii*.

Q. garryana var. *garryana* (at three different points in time: 21,000 years ago; 6,000 years ago; and, between 1951 to 2010), the evidence suggests that there has been long-term sympatry between the two across at least parts of their ranges, though they remain ecologically distinct, supporting the idea of a multispecies evolutionary complex.

Exploring further the biogeographical and ecological context, Valiente et al. explore the functional diversification amongst the North African/European oaks in *Quercus* section *Quercus* and those in *Quercus* section *Cerris*, analyzing differences in functional traits related to growth potential and drought resistance and their relationship to climate. González-Rodríguez et al., putting their noses to the ground in central Mexico, take us through the fascinating and as-yet little-studied question of what role plant/soil interactions play in the composition of oak communities and ultimately in species diversification and distribution. We learn that plants recover only a proportion of the total nitrogen and phosphorous contained in the organic matter that they return to the soil (leaf litter, etc.) – and that this proportion, known as foliar resorption efficiency (FRE), shows plastic variation depending on environmental factors, but there is also a genetic component. Previously no clear functional differences have been found between Red and White Oaks; the results of this study suggest that species-level differences may exist for nutrient recycling and thus affect oak community composition.

Photo 5/ How do oak forest communities develop? What functional traits distinguish Red and White Oaks and what is their role in the evolutionary history of the genus *Quercus*?

Although we oak lovers take for granted that hybridization exists within sections of the genus *Quercus*, Chatwin et al. ask the thoughtful question, why? In other words, what is the adaptive advantage of hybridization (for there must be one, or, at the very least, if there isn't, we must understand why)? And what role does this play in oak evolution? This complex question at the frontier between ecology and genetics finds some elements of an answer here: hybrids that in moments of stress are temporarily more "fit" than

either of the parent species, keep genes "alive" that, through later backcrosses, give the parent species a specific advantage in the face of such stress, in this case, drought. Sort of the evolutionary equivalent of not putting all your eggs in one basket.

Sork et al. take us into the fascinating realm of epigenetics, explaining how these processes can shape adaptation. The authors point out that epigenetic mechanisms, notably DNA methylation, may be particularly important for long-lived species such as oaks as they may facilitate more rapid responses to changes in the environment than genetic processes. Does the environment induce methylation? What is the within-populations natural variation in DNA methylation? Does natural selection act on that variation? These are some of the questions addressed here.

Strijk and Hinsinger explore the origin, evolution and genomic diversity of the oaks of Vietnam using a recently (2015) proposed technique for sequencing that allows for the use of suboptimal samples (such as from specimens stored in herbaria, silicagel-dried leaf samples, etc.) for genomic and evolutionary studies. Although this does raise questions about how to safeguard the integrity of the historic herbaria that are a tribute to mankind's quest to understand nature, the technique could open avenues to enhancing our knowledge of the diversity of the past and, consequently, our understanding of the present.

As you go through the myriad different stories that are told within this volume, I am sure that, like me, you will find there are those that you will want to go back to, those that add substance to your own story, those that reveal intriguing and unsuspected aspects of the world of oak, those that will forge a deeper relationship between each of us and these trees that command so much passion and interest.

I am grateful as Editor to be given the opportunity to enjoy such an intimate relationship with – if not the presenters themselves – the written contributions that represent their data, their objectives, thoughts, and creativity. On top of the time that they spend transforming all of that into prose, the volume you are holding represents about 900 hours of work and dedication to spreading the *Quercus* word.

Acknowledgments

My thanks to Tim Boland, Allen Coombes, Diana Gardener, Dirk Giseburt and Andrew Hipp for their comments and suggestions.

Photographers. Title page: Gérard Lionet. Photos 1, 2, 4a-c, 5: Béatrice Chassé. Photo 3: Maricela Rodríguez Acosta. Photo 4d: Guy Sternberg.

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