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Searching for the Hardy Southern Live Oak
Anthony Aiello
I just finished reading through the manuscripts for the Proceedings of the 8th International Oak Society Conference, and I am left with the feeling of having been taken on a long walk through the town where I went to college, but by a friend who had grown up there. At every turn I find someone or some place that I know. The background stories, however, are all new or more nuanced than I remember them. There are 25 stories in these Proceedings, each of them strange and surprising in some way. Our ancestors were caching acorns 780,000 years ago? You can extract embryos from their acorns, freeze them, then thaw them and grow an oak tree? “Truth is stranger than fiction,” Mark Twain wrote, “but it is because fiction is obliged to stick to possibilities; truth isn’t.”

There were no outlier talks at the 2015 International Oak Society Conference at The Morton Arboretum, and at the same time very little traversing of the same ground – remarkable given the ostensibly tight focus of the Conference. I heard particular ideas repeated more often at the Botany 2015 meetings this past summer, scattered though they were around all of the plant tree of life, than I did at our IOS Conference focused on a single lineage of about 450 species. This fact notwithstanding, I came away from the IOS Conference and from these Proceedings with several insights that were each illustrated in different ways by multiple talks. I am left thinking altogether differently about oaks from having read these.
The high genetic diversity of oaks may buffer them against population risks that we think of as inherent to rare species and regional endemics. In conservation genetics, we often expect that species or populations that are small, disjunct, or limited in number of individuals will have little genetic variability, and that this will pose a risk to the viability of those populations. Three articles in this volume suggest that oaks may not follow this expectation. Ashley et al. and Backs demonstrate clonality, genetic differentiation among populations, and high genetic variability within populations in both *Quercus tomentella*, a rare endemic of California’s Channel Islands, and *Q. hinckleyi*, endemic to two counties in West Texas. Similarly Deng et al. find high genetic diversity and phylogeographic structure in the rare *Q. arbutifolia* from montane cloud forests of Southern China. As so much genetic variation is present within each oak population, we probably need to adopt conservation criteria for populations that are not based solely on how much neutral genetic variation each population samples.

Oak populations, species, and ecosystems are the target of conservation projects at regional and global scales, with strong coordination among partners around the globe. Three oak conservation projects are presented, with the potential to catalyze research and interventions at the level of oak communities, populations, and species worldwide. Sun et al. describe a targeted conservation strategy for *Q. sichourensis*, part of a pilot project to conserve Yunnan’s Plant Species with Extremely Small Populations (PSESP). Darling and Fahey describe a more synthetic regional strategy for recovery of oak ecosystems in the Chicago region, entailing management, reforestation, production, and outreach and education efforts across the region. Kenny and Westwood outline The Morton Arboretum’s Global Oak Conservation Initiative, which entails an assessment of need.
and risk to individual species worldwide, coordination of in-situ and ex-situ conservation actions, and outreach and education to public and professionals. In conservation, as in research, such networks of collaborators will play an important role in ongoing efforts to save trees.

We are still discovering new ways to build and utilize oak collections, using new technologies and broader collaborative networks. Living collections are an important piece of research and conservation infrastructure (Arnet et al. 2015; Cavender et al. 2015), but they are most useful if they appropriately sample the genetic, phylogenetic, and ecological diversity of their target taxa. This year’s talks make clear that collections research has moved well beyond the acquisition of new species and cultivars. New collections and new cultivars will of course always be a focus of living collections research – Russell and Jablonski report on 11 oak cultivars new or newly described since the 2012 IOS Conference – but increasing focus is placed on understanding ecological and genetic diversity. Aiello documents a trip to find northern populations of the southern live oak, *Q. virginiana*. This echoes ongoing work to collect from winter-hardy populations of other Southeastern USA oak species (M. Lobdell, The Morton Arboretum, personal communication) and can serve as an acid-test for current ideas about assisted migration (Aitken and Bemmels 2016). These trees will presumably find their way into the multisite APGA oak collection (Paige, this volume), which has been a gift to researchers endeavoring to understand oak biodiversity and oak ecology (Kaproth and Cavender-Bares, this volume; Hipp et al. 2014; Pearse and Hipp 2014). Rodríguez-Acosta et al. then describe how they have overcome the challenges of raising oaks in Puebla, and the use of their Garden to better understand oak adaptations and oak growing in challenging environments.
Photo 3/ *Quercus insignis*

Photo 4/ *Quercus pacifica*
Three interesting new technologies are described for oak propagation and ex-situ conservation. Bassuk et al. report on a new stool bed layering technique developed for asexual production of oak hybrids and cultivars, and Rothleutner reports on an anther culturing technique useful for producing homozygous trees, especially useful in a genus in which heterozygosity and allelic diversity are the rule. Both methods may prove useful in conservation as well as development of landscape trees. Walters et al. describe ongoing research into cryopreservation of oak embryos for ex-situ conservation. Given the importance of seed banks for conservation and research (Haidet and Olwell 2015; Etterson et al. 2016), the ability to freeze oak embryos may become part of the long-term conservation strategy for endangered oak species.

**Oak species and lineages are identifiable biological entities that we can know and understand.** We have long labored under the impression that oak introgression is so rampant that our concept of species as groups of interbreeding populations does not apply at all to oaks (Burger 1975; Van Valen 1976; Petit et al. 2003). Three papers in this volume demonstrate that this impression – even anxiety – may be laid to rest. Manos demonstrates that the oak phylogeny is a recoverable entity using genome-scale data, right down to the tips, and that the oak phylogeny he and colleagues are building is far enough along to begin to erect a usable, geographically and morphologically structured classification. Gailing and Riehl argue persuasively that the genes underlying ecological diversification in European White Oaks may also shape ecological diversification and species differentiation among Red Oaks of the upper Midwest, and that natural selection on a subset of genes plays a significant role in shaping among-population and among-species genetic diversity. Sork et al. likewise demonstrate high genetic coherence of the California White Oak species: while there is remarkable hybridization, even in this difficult species complex, species across much of the oak phylogeny appear to be knowable genetic and ecological entities.

**The ecology of oaks integrates over a history of divergence among species and convergence among lineages.** We see in today’s oak species a remarkable range of trait diversity, with solutions to ecological problems occurring at deep splits in the evolutionary history of oaks (Manos et al. 1999) and at the tips of the oak tree of life (Cavender-Bares et al. 2015). Cavender-Bares synthesizes decades of literature in oak ecology and evolutionary biology to tell the story of the crucial role of American oaks in ecosystem function and human culture, and the role of ecology in shaping oak biodiversity throughout the Americas. She argues convincingly that the ecological importance and diversity of the American oaks rests in part on convergence at all levels of the oak phylogeny, shaping patterns of co-occurrence and ecological function. Kaproth and Cavender-Bares then demonstrate that these convergent oak adaptations to drought stress in different clades vary based on the intensity of drought selective pressure, and that there is a tradeoff between drought-tolerance and the ability to grow rapidly in response to increased resources. Red Oaks and White Oaks have independently optimized their allocation to drought tolerance and drought resistance. Finally, Pearse reviews the literature on oak masting (including his own contributions) to demonstrate that oak masting depends on a complex interaction between resource availability, weather cues, and pollen limitation, and that the precise mechanisms vary from species to species. Where we might previously have asked the very reasonable question, “why do oaks mast?” (Sork et al. 1993) the implication of Pearse’s paper appears to be that there is not a universal reason for oak masting: oaks have commandeered masting to answer a variety of evolutionary and ecological problems.
We are on the cusp of understanding how (and how rapidly) oak species and lineages can adapt to rapid ecological transitions. Trees – indeed, all plants – may respond to ecological transitions that tax their plasticity by dispersing or adapting or doing both (Norberg et al. 2012; Boeye et al. 2013; Booth et al. 2015). In the face of rapid climate change, understanding how trees will respond to climate change is a key to evaluating how today’s interventions may shape the biodiversity of tomorrow. Kremer presents an overview of the exciting and ambitious TREEPEACE project (http://www.treepeace.fr/), which is investigating microevolutionary changes in *Q. petraea* at scales ranging from a single generation to 10,000 years, investigating how natural selection during periods of climate change have shaped oak genes, genomes, and phenotypes. This work builds on a wealth of genomic and genetic mapping data (Bodénès et al. 2012; Lepoittevin et al. 2015; Plomion et al. 2016) to create a finely resolved genomic picture of the rate of oak adaptation. Konar et al. present a high-density genetic map of the red oak (*Q. rubra*) genome, demonstrating the power and limitations of high-throughput reduced representation genomic sequencing combined with a very creative use of two landscape oaks. Heim et al. then utilize this map to investigate the genetic underpinnings of several ecologically significant oak traits: the timing of bud burst, leaf morphology, autumn coloration, and marcescence (retention of leaves on the tree beyond their active growing period). They have created a common garden of more than 1,000 grafted plants representing 409 full siblings from a single mother tree, which should provide material for years of genetic study. These studies will lay the groundwork for understanding the genetic structure of adaptation in oaks, and may well scale up to meet phylogenetic studies of climate change adaptation (e.g., Pearse and Hipp 2012).

Oaks have had a profound effect on human culture. Few readers of this Journal will doubt that oaks have deeply impacted human culture and evolution (if you do, please read Logan 2005), but the three ethnobotanical studies presented here span a particularly wide range of time scales. From the past century, Kay recounts the story of oak-rod basketmaking in Brown County, Indiana, focusing on three of the last practitioners of the craft. Their work can still be seen today. Sternberg then tells the fascinating story of the
Athens Pathfinder, a white oak (*Q. alba*) that sprouted in the early 1700s and fell in 2008: the tree may have been Illinois’s last standing trail tree. Finally, Chassé tells the long story of acorn eating throughout human history, from 780,000 years ago to the present day, arguing convincingly that acorns have been a much more important part of human diet than we have previously thought.

I expect that as you read through these papers, you’ll come away with an altogether different set of insights than I did. Most of you reading this Journal have been thinking critically about oaks for a longer time than I have. I hope, however, that whatever your background, you have the time to read through these papers back-to-back, in a few sittings, and appreciate what a lot of landscape is covered here. It’s fun and exciting to see how our understanding of oaks is growing. I can’t wait to see what the next 20 years – even just the next field season! – brings.

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