FOREWORD

Ode to the Diversity of Oaks and Their Resistance to Dark Times

Looking out my window in snowy New England, the *Quercus rubra* (northern red oak) I see are in high abundance. In the fall, they drop their leaves and in the spring they flush them again. Large xylem vessels and phloem cells are constructed each spring to rapidly nourish bud break and the unfolding of miniature leaves into fully-formed light-harvesting marvels; their tiny stomate mouths open wide releasing streams of water vapor, the cost of pulling carbon dioxide molecules from the air, which also releases oxygen. The breathing and nourishment of the oaks that dominate Northern Hemisphere forests are critical to our life-support systems. Maybe you join me in thinking deeply about the future of oaks and what human societies of the Anthropocene can do to create resilient forests in dynamic environments. What I love most about the oaks, and what has kept me fascinated by them since I was a child, is their diversity. They are all very oaky, but yet all so very different. In considering how humans can actively guide our forests, pondering how they came to be so diverse seems essential.

The American oaks – the ones that have surrounded me since my earliest memories – come first into view for me. Curiously, the bristle-tipped Red Oaks (section *Lobatae*) and their roundly lobed White Oak siblings (section *Quercus*) are frequently in close proximity. It now seems that the adaptive capacity of these two lineages to withstand freezing was critical to their proliferation in North America.[1] The sections *Lobatae* and *Quercus* that evolved deciduousness each comprise well over a hundred species. In contrast, the evergreen oaks of sections *Protobalanus*, *Ponticae,* and *Virentes* (which, like sections *Lobatae* and *Quercus*, are in subgenus *Quercus*) inhabit mild climates in coastal regions or southern latitudes and include very few species. The capacity to go dormant was likely essential to the oak migration some 60 million years ago when land bridges enabled pathways at high latitudes to the North American continent. At high latitudes, the world goes dark for months. There is no light to energize chlorophyll. Vulnerable leaves that expose trees to the elements are a liability. Unlike their *Lithocarpus* (stone oak) relatives, oaks had already adapted to a life cycle of intense photosynthesis followed by dormancy to survive the inhospitable period. This enabled them to massively diversify during and after

1. Fontes, C.G., J.E. Meireles, A.L. Hipp, and J. Cavender-Bares. 2025. Adaptive Evolution of Freezing Tolerance in Oaks Is Key to Their Dominance in North America. *Ecology Letters*, 28: e70084. https://doi-org.

the Eocene-Oligocene transition when the climate cooled and dried, giving rise to the temperate forests of North America.

The consistent coexistence of the Red and White Oaks across the continent remains a puzzle. Do the White Oaks set up the conditions for the Red Oaks to invade by creating ectomycorrhizal soils and nutrient-rich leaf litter? Do fungal pathogens like *Bretziella fagacearum* (oak wilt) keep the faster spreading but more vulnerable Red Oaks in check? These mechanisms remain elusive, yet a great source of their resilience is surely their diversity and capacity to coexist. Species of different lineages appear to perform better and grow faster together than alone. Diversity is critical to resilience at many levels. Genetic diversity within species reduces the risk of disease and provides the capacity for adaptation through gene exchange across the syngameon of related oak species. The need for diversity is a rallying cry because it provides a wide portfolio of options in the face of many risks. I have watched the *Q. macrocarpa* (bur oak) that we selected from different populations and planted in common gardens across latitudes resist various stresses differently.[2] Listening to my colleagues across academia, decisionmakers on the land, and forest practitioners in many realms, I am now convinced that we can no longer be passive bystanders of our forests. With so much change unfolding before us, assisted gene flow and planting diverse forests fortified with numerous native trees, emphasizing oak species and genotypes, will give forests an increased chance of resilience. Following the path nature has showed us, planting Red and White Oaks together is critical. So too is planting diverse genotypes that can withstand different stresses.

In these turbulent times, I seek inspiration from my oak friends. Oaks have found many ways to resist upheaval. On the Atlantic front, Live Oaks (section *Virentes*) can resist hurricanes with shifting winds in every direction. When the atmosphere and soil are parched, oak vascular systems in species like *Q. emoryi* (Emory oak; section *Lobatae*) in Arizona or *Q. dumosa* (coastal sage scrub oak; section *Quercus*) in California can resist enormous tensions. Even when their large vessels cavitate, others continue to operate, perhaps resorting to tiny, hidden vasicentric tracheids to keep water flowing. Even when cut, an oak tree can resprout from the base. It is not so easy to kill an oak. Or they wait it out. Seedlings live quietly in the understory, surviving initially from cotyledon stores, until their opening moment comes. Many millions of years ago, oaks came to the North American continent expanding the realm where they could persist. Diversity and adaptability enabled them to succeed. Doing our part to support diverse oak-dominated forests is critical to our life support systems and our own well-being.

It is time to help.

How do we create a generation of tree planters eager to foster resilient forests, giving back to our planet in this time of need? How do we create the financial resource base to plant resilient forests and care for them? Incentivizing the next generation to take on the important and meaningful work of assisting nature to enhance forest diversity and resilience is a central pillar we can foster through our passion and concern for the future.

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2. Rea, L.M.S., L. Ostrowsky, R. Mohn, M. Garner, L. Worcester, C. Lapadat, H.R. McCarthy, A.L. Hipp, and J. Cavender Bares. 2024. Genetically based variation in fitness and carbon assimilation among bur oak populations. *bioRxiv* 2024, 2024.2010.2030.620350. DOI: 10.1101/2024.10.30.620350.