Evolving on two fronts:
Oak species and syngameons

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Abstract

William 'Bill' Burger wrote in 1975, "I believe that the classical species-concept in *Quercus* defines a very real population system and that it evolves on two fronts. One is that of continuing to adapt to a niche that differs slightly from its close relations. The second is in sharing the broader evolutionary advances of these same close relations that together comprise the genetically isolated biological species." Burger's view of oak species reflected morphological study going back at least to 1947, but since Burger's time, ecological and genomic data have accrued to further support his hypothesis: oak species are distinctive ecologically, morphologically, and genomically, but interspecific gene flow moves alleles (gene copies) between species. This movement of alleles between species is called introgression. Introgression increases genetic variation within species and shuffles alleles into new ecological contexts, where they may shape the evolution of the species they enter. Thus natural selection working on a single population does so by grabbing hold of innovations (alleles) that evolved in many species—the suite of interbreeding species that constitute an oak syngameon. In this essay, I discuss Bill Burger's species concept and ask how it aligns with what we know about oak species today.

Keywords: Adaptation, genomics, hybridization, introgression, species concepts, syngameon

Plant taxonomist William 'Bill' Burger started his graduate studies in Botany at Cornell University in 1956. As a student, he read Karl Wiegand's (1935) "A taxonomist's experience with hybrids in the wild." In this article, Wiegand, the former head of Cornell's botany department and early director of their herbarium, noted how botanists' impressions of the prevalence of hybrids had changed over time, from the first edition of Gray's *Manual of the Botany of the Northern United States*, in which two hybrids were listed in the genus *Quercus*, to the growing realization that spontaneous (natural) hybrids were common in many genera, particularly oaks. But Wiegand viewed hybrids "like swarms of bees, buzzing around for a time, only to disappear" (pp. 165–166), of little importance to the evolution of species. Wiegand's view would turn out to be a hybrid itself, between 19th-century and 21st-century understandings of species.

Wiegand referred to two hybridizing oak species in his lecture: *Quercus macrocarpa* and *Q. bicolor*. Just three years later, Edgar Anderson would introduce the term "introgression" to describe the movement of genes between species (Anderson and Hubricht 1938), arguing that genetic variation due to introgression is important fodder for evolution. Anderson spoke little if at all about oaks in his published work, but he noted hybrids between *Q. macrocarpa* and *Q. bicolor* and mentioned them to colleagues (pers. comm. in Stebbins 1950 p. 64). William Trelease discussed the possibility of hybridization between *Quercus macrocarpa* and *Q. bicolor* in his foundational (1924) taxonomic treatment of the American oaks, and hybrids between them were noted in Ernest Palmer's (1948) review of oak hybrids. Burger was thus in good company when he began his graduate studies of hybridization in *Q. macrocarpa* and *Q. bicolor*.

Burger selected for his graduate work four natural areas near Ithaca where Wiegand and others had collected *Q. bicolor*. Two sites were of particular interest: herbarium specimens suggested hybrids as early as 1915 at South Hill Swamp and 1895 at Renwick Woods. At each site, Burger identified and mapped all *Q. macrocarpa* and *Q. bicolor* taller than 1 m and sampled leaves from about 10% of them. From each of 12 leaves per tree, he measured petiole length, leaf length and width, depth of the second and third sinus, and the distance from the midvein to the base of the sinus. He plotted values of these traits against each other to see how individuals clustered morphologically. He expected that individuals of a single species would cluster together and that hybrid individuals would cluster at or beyond the margin of a species cluster.

Burger found ecological and morphological distinctions between *Q. macrocarpa* and *Q. bicolor*, but minimal reproductive barriers between them: morphological intermediates were present at both of the sites where hybrids had previously been found. He inferred from this that the two species could interbreed freely under natural conditions. The presumed hybrids seemed as healthy as the presumed “pure” species, and acorns from hybrids germinated as readily as acorns from the pure species. Burger suspected, in fact, that genes from local *Q. macrocarpa* were likelier to find their way into local *Q. bicolor* than into *Q. macrocarpa* from more distant counties (Burger 1959 pp. 66–67).

Burger nonetheless maintained that the entities we call oak species were real. He felt, as Verne Grant had written a few years earlier, that interbreeding oaks were “not good species in the usual sense, because they interbreed freely with each other,” but that the morphology of relatively pure individuals was “equivalent to that of good species” (Grant 1957, in Burger 1959 p. 64). Hybridization alone was not enough to undermine centuries of taxonomic work. For Burger, classical oak species were real. He was not yet able, however, to express why or even precisely how classical oak species were real, except that they were recognizable.

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Burger was working against the backdrop of the “Biological Species Concept,” a reproductive definition of species that was introduced by Edward Poulton, an early apologist for Darwinian natural selection, 120 years ago; updated in modern genetic and evolutionary terms by Theodosius Dobzhansky 30 years later; then placed into a more explicit geographic and taxonomic context and dubbed “The Biological Species Concept” by Ernst Mayr in 1942. According to Mayr’s Biological Species Concept, “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” Species are species according to the Biological Species Concept because they don’t hybridize with one another readily in nature. For Burger, the Biological Species Concept was difficult to reconcile with the frequent hybridization he observed between traditional oak species.

In 1975, Burger revisited his thesis in a paper entitled “The species concept in *Quercus*” (Burger 1975). In this paper, he described “classical” oak species: “An example of a typical classical species-concept is *Quercus macrocarpa* Michaux of eastern North America. This species is readily recognized by its deeply lobed lyrate leaves, the acorn cup with fringed edge, and a host of more subtle characters such as tree-form, bark of trunk, and bark of the smaller stems. In addition, *Q. macrocarpa* can often be characterized by its habitat in a given region. The species is easily recognized throughout its large range but it does contain considerable geographic variation. It is a species so well known that its most common name, the bur oak, has been used as a name for counties and towns” (Burger 1975 p. 46). Classical oak species were ecologically and morphologically recognizable entities, despite the fact that they often covered wide geographic ranges.

But what appeared to Burger to be pretty free mating between *Q. macrocarpa* and *Q. bicolor* raised the question of what kind of biological entity classical oak species were. Burger believed that if you are serious about the Biological Species Concept, you'd have to consider all or nearly all of the white oaks (*Quercus* sect. *Quercus*) as one "biological species," because they appear to all be interfertile. In fact, if we follow Burger's reasoning, we'd have toss in at least some of the live oaks and deer oaks, *Q.* sections *Virentes* and *Ponticae*, as well, as they interbreed with members of sect. *Quercus*. Then we could keep the intermediate oaks (sect. *Protobalanus*) and the red oaks (*sect.* Lobatae) as separate biological species. That would consolidate the roughly 250—300 classical oak species of the Americas into perhaps three biological species.

This would certainly make taxonomy easier, but at the cost of throwing away a lot of information. "We continue to function taxonomically with our classical concepts and they continue to perform their duties of identifying morphological and ecological correlations for the purposes of storing and retrieving information" (Burger 1975 p. 46). Even if they aren't good "Biological Species" in Mayr's sense, we recognize classical oak species on our walks and in our herbaria. What, then, are they?

Burger offered an answer: "I believe that the classical species-concept in *Quercus* defines a very real population system and that it evolves on two fronts. One is that of continuing to adapt to a niche that differs slightly from its close relations. The second is in sharing the broader evolutionary advances of these same close relations that together comprise the genetically isolated biological species. Both the classical and biological concepts represent real population systems in *Quercus*" (Burger 1975 p. 48). This description of the "classical species concept" in oaks contains three elements that together comprise what I take to be Burger's view of oak species:

1. Groups of interbreeding classical oak species form "genetically isolated biological species." The classical species we recognize are nested within these larger "biological species."

There are groups of species in oaks that constitute reproductively interconnected "population systems" that are isolated from other such groups. Burger calls out *Quercus* sect. *Quercus*, which contains *Q. macrocarpa* and *Q. bicolor* and is reproductively isolated from other such groups, such as the red oaks (*Q.* sect. *Lobatae*). Nested within “biological species” such as *Q.* sect. *Quercus* are “classical” oak species, the ones that we recognize and name: *Q. macrocarpa*, *Q. bicolor*, and all the others.

2. The “classical species-concept in *Quercus* defines a very real population” that “continues to adapt to a niche that differs slightly from its close relations.”

Burger uses the term “population” variously to refer to three different kinds of entities: (a) local groups of individual plants that all derive from a single classical species or represent a hybrid mix of more than one, as in “occasional problematic populations of mixed origin” (p. 45); (b) “classical species,” groups of populations that evolve collectively and are, in oaks at least, “generally easy of recognition and not genetically isolated” (p. 49); and (c) “biological species,” groups of interbreeding populations that may comprise two or more “classical species.”

In sense (a), individuals of a population share geography, habitat, and the landscape history of the place where they currently grow. In sense (b), individuals of a population share an ecological and morphological “recognizability” and evolutionary trajectory. In sense (c), individuals of a population can cross-pollinate and fertilize each other’s ovules. For Burger, “biological species” (e.g., *Quercus* sect. *Quercus*) are populations in sense (c). The “classical species” contained within them (e.g., *Q. macrocarpa* and *Q. bicolor*) are populations in sense (b). These come together to form reproductively interconnected groups of individuals in single forests, populations in sense (a).

Ecological niche is central to Burger’s view of classical oak species. Classical oak species in his view have unique “morphological and ecological correlations” (p. 46). They are “defined by different ecological parameters” (p. 47). They form “functioning ecological unit[s] in nature” (p. 48). Each classical oak species is, for Burger, defined and maintained by its unique niche (cf. Van Valen 1976).

3. Classical oak species "shar[e] the broader evolutionary advances of these same close relations that together comprise the genetically isolated biological species."

For Burger, classical oak species "share… evolutionary advances" by passing them around within the larger "biological species." In other words, classical species share the adaptations they have evolved in their separate niches through interspecific hybridization.

Put these three elements together, and you get Burger's view of oak species. When we use the names *Q. macrocarpa*, *Q. bicolor*, or any of the hundreds of other classical oak species names, we are talking about ecologically and morphologically distinct populations that evolve collectively through introgression. Oak species, Burger tells us, evolve on two fronts: each classical species evolves adaptations to its own niche, and sets of classical species are embedded within "biological species," allowing classical species to share evolved adaptations by hybridization and introgression with others in their "biological species."

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Was Burger right? Are the entities we call "species" in oaks reproductively intertwined with one another, "classical species" nested within "biological species"? Are they uniquely adapted, each to its own niche, differentiated from close relatives? Do they exchange adaptive alleles? At the time that Burger was writing, there was some evidence for all of these claims, particularly the first two. But the advent of genomic data has given us the ability to rigorously test claims one and three, and ecological work over the past two decades demonstrates numerous tradeoffs that shape niche partitioning among close oak relatives (claim 2). Burger's views have been largely borne out.

1. Oak species form syngameons.

Oaks hybridize while also remaining distinct morphologically, ecologically, and genomically (Kremer and Hipp 2020, Hipp 2024 chaps. 3, 6 and refs therein), even over the course of hundreds of generations of interbreeding (Stebbins et al. 1947). Thus natural hybridization in oaks does not appear to undermine species distinctions (Hipp 2015).

Oaks often grow in multispecies communities (Cavender-Bares et al. 2018) in which classical species can hybridize and their hybrid offspring can backcross to one parent species or the other (e.g., Ribicoff et al. 2025). This phenomenon has the effect of producing offspring that, after several generations of backcrossing, look like one parental species but carry many alleles of the other due to the initial hybridization. Hybridization and introgression of alleles among numerous co-occurring species produces what we call a syngameon. The term syngameon refers to *a group of species that interbreed but nonetheless remain distinct as species* (Grant 1971, Hardin 1975, Cannon and Petit 2020, Hipp 2024 pp. 224–5, Cavender-Bares 2025). Syngameons are well studied in several tree groups, including pines, spruces, rhododendrons, willows, birches, and tropical trees (e.g., Cannon and Lerdau 2019, Whittemore and Miller 2023, Guo et al. 2025). They are known across the tree of life, in clades that range from corals to beetles and butterflies to humans (reviewed in Boecklen 2017, Buck and Flores-Rentería 2022). Burger's network of interbreeding "classical" oak species within a larger "biological species" is a syngameon.

Oaks around the world have tended to evolve low to moderate barriers to interspecific reproduction (Abadie et al. 2012, Lepais et al. 2013). As a consequence, many species can cross with distantly related oak species, the most recent common ancestors between hybridizing species being 20 million years old or older in some cases (Zhou et al. 2022). Introgression in multispecies oak communities is moderated by pollen competition, which results in reduced hybridization as the number of individuals per species in a forest stand becomes more balanced (Klein et al. 2017). Introgression is also counteracted in part by ecological selection, which tends to maintain genetic distinctions between ecological distinct species

(Muller 1952, Swenson et al. 2008, Wu et al. 2024, Zimmermann et al. 2025). The result is that each oak syngameon is patchy on the landscape, shaped by demography (Lepais et al. 2009), ecological conditions (Reutimann et al. 2023), and attenuation of population sizes or shifting ecological conditions at range margins (Nagamitsu et al. 2020, Ribicoff et al. 2025, Parker et al. n.d.).

We do not know the relative importance of physiological reproductive barriers (both prezygotic and postzygotic) compared to ecological selection against F1s in maintaining oak syngameons. We also don't know whether oak syngameons are an outcome of selection favoring porous species boundaries (Barraclough 2024). Whatever we learn about these issues and others in the coming years, Burger's first point holds: "classical oak species"—the ones we've been recognizing for centuries if not millennia—are maintained within broader "biological species," syngameons.

2. Oak species are adapted to ecological niches that are distinct from those of their close relatives.

Closely related oaks tend to differ in habitat, at least slightly (Muller 1952, Bourdeau 1954). Thus niche differentiation shapes the diversity and composition of oak-dominated communities along gradients of soil type, moisture availability, vegetation, climate, and elevation (e.g., Whittaker 1969, Spellenberg et al. 1998). Research by IOS member Jeannine Cavender-Bares beginning in the early 2000s showed that niche differentiation in oaks is strongly shaped by evolutionary history, particularly in the Americas: closely related white and red oak species have diverged to occupy different areas of niche space, while distantly related species in the red and white oak sections have converged to live in similar habitats (e.g., Cavender-Bares et al. 2004, 2018).

These niche differences are the adaptations that Burger wrote about. Oak species have evolved trade-offs between fire-tolerance and growth rate that differentiate closely related species of Florida (Cavender-Bares et al. 2004) and the Chihuahuan sky islands in Texas (Schwilk et al. 2013). Evolved variation in drought and freezing tolerance separates closely related species along temperature and water-availability gradients (Kaproth et al. 2023, Fontes et al. 2025). Evolved differences in fine root architecture (McCormack et al. 2021), leaf morphology (Ramírez-Valiente et al. 2020), and the balance between desiccation resistance and drought avoidance (Fallon and Cavender-Bares 2018) differentiate oak species along drought gradients.

It remains to be seen how distantly related oak species co-occur without excluding each other competitively (Cavender-Bares 2019), and we still do not know how important niche differentiation is to the maintenance of species boundaries. But Burger's impression that oak species "adapt to a niche that differs slightly from its close relations" is supported by contemporary research.

3. Oak species share adaptive alleles with one another through introgression.

Long before genome sequencing, Cornelius Muller hypothesized that interspecific gene flow could drive oak speciation and species migration (Muller 1952 fig. 3). It turns out he was right for at least some species: genomic evidence suggests that the *Quercus petraea* migrated northward as the glaciers receded by means of pollen, introgressing into *Q. robur* populations that established first (Petit et al. 2003). Selective maintenance or introgression of *Q. robur* alleles into *Q. petraea* then allowed *Q. petraea* to persist in cool climates (Leroy et al. 2020). Edgar Anderson argued that the slightest "trickle of genes" between species might be of profound importance to the genetic diversity of species (Anderson 1949 ch. 5 [esp. p. 62]). It turns out he was correct, as well: gene flow from *Q. berberidifolia* into *Q. engelmannii* increased genetic diversity of the latter and may have allowed *Q. engelmannii* to adapt to the Mediterranean climate of southern California (O'Donnell et al. 2021).

Adaptive introgression appears to be widespread in *Quercus*. Genomic data show signals of adaptive introgression between lineages in Eurasia and the southeastern U.S. (Zhou et al. 2022). Across several species, introgressed regions of the genome are associated with climate and local environments, suggesting a role for introgression in local adaptation (Nagamitsu et al. 2020, Fu et al. 2022, Liang et al.

2025). It seems likely that wherever we find introgression (Burger's point 1) and ecological specialization (Burger's point 2 in a context of high sympatric oak species diversity (Cavender-Bares et al. 2018), we will find that Burger's final point was right: oak species share evolutionary innovations, the "broader evolutionary advances" of their respective syngameons (Burger's point 3).

We have much to learn about the importance of oak introgression, as studies to date fall short of experimentally connecting success (fitness) of oak populations to the presence of particular genes or genomic regions they have gained from other species by introgression. It nonetheless seems safe to say that Burger was right about the adaptive significance of oak introgression. Each oak syngameon is a system of populations in which numerous species contribute to each other's evolution. The syngameon is "more than the sum of the parts" in the words of Chuck Cannon and Rémy Petit (2020), and oak species as a consequence evolve "on two fronts," both individually and as part of a syngameon.

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For Burger, species are the populations of individuals we find on the landscape that are ecologically, genomically, and (hopefully) morphologically similar to one another and more or less discontinuous with others. They are the kinds of species referenced in the genomic cluster species concept (Mallet 1995) and Rieseberg's (2006) classic investigation of the nature of plant species. They are the genotypic or phenotypic clusters we mean when we talk about species and speciation. When we say *Quercus macrocarpa*, most of us don't track pollen flow in our minds; instead, we imagine individual trees that look like, grow in the same habitats as, and are genetically similar to the other individual trees we call *Quercus macrocarpa*. Species are distinct from, or discontinuous with, other species (Whittemore 1993). This discontinuity is what the researchers of the Modern Synthesis were trying to explain as they laid out a response to the question, "what is a species?" (Stebbins 1950 and references therein). Without having access to the genome, Burger was nonetheless clear that evolved ecological discontinuities build the fences by which we recognize species.

Bill Burger sent me an email in April 2019, 60 years after depositing his Master's thesis, about some of the things we were learning about the oak phylogeny at the time. He wrote, "ZOWEEE! Yes, the 'species' do remain 'coherent' despite their improper behavior!... Nature (every part of it) seems to be much more complex than we had at first thought. Of course, all your efforts carry a 'carbon footprint' that is contributing to the certain collapse of our completely unsustainable culture (I figure well before the end of the century). Don't worry about our species; we will be there with the rats and roaches (only not many of us). But getting on a Jet Aircraft to visit more distant OAK populations identifies YOU as a significant contributor to Global Storming… But isn't it one helluva blast! What we are learning about our planet and its biota is mind-boggling."

After a career researching tropical plant taxonomy and plant biodiversity, Bill Burger spent the last decades of his life photographing the natural world and writing popular science books that exude his passion for the natural world. He died the Sunday after Thanksgiving, 2022, leaving us a vivid example of what it looks like to evolve on two fronts, both as a human and as a scientist.

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heavily pruned in this essay for reasons of space; for a fuller reference list, see version 1 of this manuscript on EcoEvoRXiv (https://doi.org/10.32942/X2M64S; https://ecoevorxiv.org/repository/object/11178/download/20330/).

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