Evolving on two fronts: Bill Burger on the nature of oak species

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Abstract

William 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, molecular 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 process of genetic 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 interfertile oak species act as a kind of an extended workshop for evolution, where natural selection on a single population can take advantage of innovations that evolved in multiple species. 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

Plant taxonomist William ‘Bill’ Burger started his Masters work in Botany at Cornell University in 1956. As a student, he held the position of Herbarium Assistant in the Wiegand Herbarium and read Karl Wiegand’s (1935) “A taxonomist’s experience with hybrids in the wild.” In this lecture, Wiegand—as head of Cornell’s botany department and outgoing chairman of the botanical section of AAAS—noted how people’s 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* (Gray and Sullivant 1848) in which two hybrids were listed in the genus *Quercus*, both reported to be “founded on” a single tree or individual; to the broad recognition of the feasibility of hybridization through the rediscovery of Mendel’s work; to the growing realization that hybrids were relatively common in nature in some genera, often in disturbed habitats. He discussed hybrids in *Crataegus*, *Amelanchier*, and other genera. He noted that hybrid speciation appeared to be rare. Hybridization appeared to Wiegand to be a relatively common but largely ephemeral phenomenon. “The hybrids seem like swarms of bees, buzzing around for a time, only to disappear, leaving the fundamental species to continue through the ages… I can not [sic.] help but see at least a practical difference between the causal [sic.] more or less evanescent and temporary hybrid and the fundamental established species reaching back perhaps to the glacial epoch or beyond" (pp. 165—166).

Wiegand's essay was important for calling out the fact that botanists recognized hybridization as a real phenomenon in wild plant populations, but he viewed hybrids as more or less transient and probably of limited importance to the evolution of species except for comparatively rare species of hybrid origin. Wiegand referred to two hybridizing oak species in his lecture: bur oak (*Quercus macrocarpa* Michx.) and swamp white oak (*Q. bicolor* Willd.). Just three years later, Edgar Anderson would introduce the term "introgression" to describe the movement of genes between species by means of hybridization and backcrossing and argue that in many cases, hybridization will introduce more genetic variation into a population than mutation can (Anderson and Hubricht 1938 p. 401). Anderson would later go on to mention hybrids in the bur oak and swamp white oak, though he did not publish these observation (pers. comm. in Stebbins 1950 p. 64). Wiegand and Anderson were not the only ones to recognize that these two species hybridized; the species were suspected by William Trelease (1924) to be close relatives that could hybridize and placed together as the only two members of his *Macrocarpae* group, and hybrids between them were noted by Palmer (1948). Bill Burger, working in the late 1950s and likely inspired by both Anderson and Wiegand, was in good company when he undertook for his master's work an investigation of morphological variation and hybridization in bur oak and swamp white oak.

Burger selected four natural areas near Ithaca where Wiegand and others had collected the species. Two sites were of particular interest: herbarium specimens suggested hybrids going back to at least 1915 at South Hill Swamp, and to at least 1895 at Renwick Woods. At each site, Burger identified and mapped all the bur oak and swamp white oak trees taller than 1 m and randomly selected about 10% of them for leaf sampling (a total of 54 trees at South Hill Swamp, including 10 putative hybrids but, surprisingly, no *Q. macrocarpa* that he could find; and 62 at Renwick Woods, including 6 putative hybrids and 3 *Q. macrocarpa*). From each of 12 leaves per tree, he measured a set of traits: 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. The second sinus depth was particularly useful, as it segregated nicely between the two species. Burger asked a basic question: are these two entities we have named "bur oak" and "swamp white oak" morphologically distinct? Are they good species?

Burger found good ecological and morphological distinctions between the species, but no obvious reproductive barriers between them. When the two were growing together, they seemed to interbreed freely. Burger found no evidence of reduced vigor in the presumed hybrids. Acorns collected from the hybrids germinated as readily as acorns from the pure species. Burger concluded that the two species were reproductively interconnected. Moreover, he suspected that populations of bur oak were no more reproductively connected than they were with populations of local swamp white oak. "The writer believes," Burger wrote, "that genetic material from *Q. macrocarpa* here at Ithaca has greater probability of entering the *Q. bicolor* populations in this area than it has of reaching *Q. macrocarpa* populations in Indiana" (Burger 1959 pp. 66–67), a point that would be restated in almost exactly these words by Leigh Van Valen 17 years later (Van Valen 1976).

But Burger maintained that the entities we call oak species—things like *Q. macrocarpa*, *Q. robur*, *Q. acutissima, Q. ilex*—were nonetheless real. At the time he wrote his thesis, Burger seemed unable to express in what way oak species were real. He felt, as Verne Grant had written just a few years earlier, that interbreeding groups of species like oaks were “not good species in the usual sense, because they interbreed freely with each other… [but] extreme forms show partial reproductive isolation from one another and have attained a degree of morphological differentiation equivalent to that of good species…” (Grant 1957, in Burger 1959 p. 64). Burger was persuaded that hybridization was not enough to undermine centuries of taxonomic work and his and Wiegand’s and others’ experience of oak species in the field. “In the event that hybridization does occur frequently among a number of the white oaks, as appears to be the case, the writer would prefer to retain the species names in use rather than consider them as subspecies of a broader, genetically defined species” (p. 66). He was just not yet prepared to say what an oak species is.

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Burger was working against the backdrop of the “Biological Species Concept” (sometimes abbreviated “BSC”), a reproductive definition of species that was formalized by Edward Poulton, an early apologist for Darwinian natural selection, 120 years ago; updated in modern genetic and evolutionary terms by leading scientist of the Modern Synthesis Theodosius Dobzhansky 90 years ago; and given a more geographic and taxonomic spin, as well as the name “The Biological Species Concept,” by Ernst Mayr in 1942 (Poulton 1904, Dobzhansky 1937, Mayr 1942). Under the BSC, “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” This definition from Ernst Mayr’s most well-known articulation of the species concept accords closely with what many of us learned in high school and college. Species are species according to the BSC because they don’t hybridize readily in nature. Burger wasn’t the first to discuss hybrids in oaks, but his thesis did articulate a point that I think most taxonomists feel: the biological species concept is difficult to reconcile with the frequent hybridization we find in oaks.[1]

It took Burger about 15 years to publish an explanation of what he thought oak species might actually be. In 1975, Burger revisited his thesis in a paper entitled “The species concept in *Quercus*” (Burger 1975). In this paper, he describes bur oak as a very typical “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, which often—as in bur oak—covered wide geographic ranges.

But what appeared to Burger to be pretty free reproduction between bur oak and swamp white oak raised the question of what kind of biological entity oak species were. Burger believed that if you are serious about the BSC, you’d have to consider all (or nearly all) of the white oaks (*Quercus* sect. *Quercus*) as one “biological species,” because they appear to be mostly all crossable. In fact, if we follow Burger’s

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[1] Note that Coyne and Orr (2004 p. 43) argue that in fact oaks are probably very good biological species, arguing that hybridization is not as common in oaks as suspected. However, they were making this argument just as a great deal of genomic data was about to become available, showing frequent introgression in a wide range of oak species (reviewed in Hipp 2024 chapter 3).

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. So for the Americas, that would give us perhaps three biological species for the roughly 250—300 classical oak species of the Americas. This would certainly make taxonomy easier.

We would, however, be 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 Burger's take on oak species:

1. Each reproductively-interconnected group of oak species forms a single "genetically isolated biological species," comprising multiple "classical species."

There are groups of species in oaks that constitute reproductively interconnected "population systems" that are isolated from other such groups. Without using the terms "section," "lineage," or "clade," Burger calls out the white oaks here, *Quercus* sect. *Quercus*, which are reproductively isolated from other such groups, such as the red oaks (*Q.* sect. *Lobatae*). Nested within these big "biological species" (e.g., the white oak group) are "classical" oak species, the ones that we recognize: bur oak, pedunculate oak (*Quercus robur* L.), 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's use of "population" is a little confusing, as he uses the term variously in his essay 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 are evolving collectively (how exactly is not specified) and, in oaks at least, "generally easy of recognition and not genetically isolated" (p. 49), mostly referred to in Burger's article as "population systems"; and (c) "biological species," groups of interbreeding populations that may include "classical species."

The common thread in all three of these uses of the term "population" is that members of a population share some aspect of their biology or history that members outside the population do not. In sense (a), all individuals share geography, habitat, and the landscape history of the place. In sense (b), all individuals share an ecological and morphological "recognizability" and evolutionary trajectory (which is not well defined). In sense (c), individuals are part of a reproductive group: they may exchange pollen and fertilize each other's ovules. For Burger, both "biological species" (e.g., *Quercus* sect. *Quercus*) and the "classical species" contained within them (e.g., bur oak, swamp white oak) "represent real population systems in *Quercus*" (p. 48). The oak species that we have given names to such as "bur oak" are populations in sense (b).

Ecology is central to Burger's view of classical oak species, which have unique "morphological and ecological correlations" (p. 46), are "defined by different ecological parameters" (p. 47), and form "functioning ecological unit[s] in nature" (p. 48).[2] Classical oak species are recognizable ecologically and morphologically and constantly adapting to their environment. Classical oak species are, for Burger, uniquely adapted to their niche, an argument that would be made more strongly the following year by Leigh Van Valen in his ecological species concept paper (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."

This claim is a little ambiguous, as "sharing" has at least two senses: going through experiences together (e.g., oak species evolving in similar ways to the shared environmental conditions of the Pleistocene) versus using a single common resource collectively. In the context of Burger's overall argument, in which the white oaks comprise a single "genetically isolated biological species," it seems he has in mind the second meaning above: oaks "share… evolutionary advances" in the sense in which we share secrets or jelly beans: by passing them around. The only way for organisms to do this is through gene copies, or alleles. "Classical" oak species are not defined by reproductive isolation, as Mayr thought species were; they are defined by ecology, and they share the adaptations they have developed through interspecific hybridization.

So Burger is arguing that when we use the terms "bur oak," "pedunculate oak," or any of the hundreds of other classical oak species names, we are talking about (1) interbreeding but (2) ecologically distinct populations that (3) exchange adaptive alleles. Oaks form ecologically and morphologically good species that evolve collectively through introgression. Oak species, Burger tells us, evolve on two fronts: each "classical species" evolves adaptations to its own niche, and all "classical species" embedded within a single "biological species" share these evolved adaptations.

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Was Burger right? Are the entities we call "species" in oaks reproductively interconnected? 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 some evidence for all of these claims, particularly the first two. But the advent of genomic data has given us the ability to test claims one and three more

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[2] Additionally, Burger compares *Ficus* (the figs) to *Quercus*, saying "most species of *Ficus* are genetically isolated but they possess morphological differences and play ecological roles very similar to that of *Q. macrocarpa*." While Burger does not explain "ecological roles," in the context of the article it appears as though he means simply that *Ficus* species are ecologically distinct from each other. He also makes clear that the similarity between the "ecological roles" of species in the two genera is in spite of the fact that *Ficus* species do not appear to introgress at nearly the rate that *Quercus* species do (which seems to be borne out in more recent research, which shows relatively episodic hybridization in Ficus rather than ongoing syngameon dynamics; Gardner et al. 2023). Thus: "The species of *Ficus* are not at all comparable, ecologically or morphologically, to the larger genetically defined biological species to which *Q. macrocarpa* belongs" (p. 48).

rigorously, and ecological work over the past two decades demonstrates numerous tradeoffs that shape niche partitioning among close oak relatives. It looks as though Burger's view was largely correct.

1. Oak species form syngameons

Oaks hybridize while also remaining distinct morphologically, ecologically, and genomically (Trelease 1917, Palmer 1948, Muller 1952, Tucker 1961, Hardin 1975, Whittemore and Schaal 1991, Hipp 2015, 2024 chaps. 3, 6, Kremer and Hipp 2020, Lazic et al. 2021, Rauschendorfer et al. 2022). Oaks hybridizing in natural populations can maintain their ecological and morphological distinctiveness even over the course of hundreds of generations of interbreeding (Stebbins et al. 1947, Howard et al. 1997, Wu et al. 2024). Thus natural hybridization in oaks does not appear to undermine species distinctions.

Oaks grow in multispecies communities (Cavender-Bares et al. 2018, Cannon et al. 2024) where numerous species can hybridize and their offspring can subsequently mate back to the parental species (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 hybridization event that occurred a few generations back. These alleles are said to introgress from one species to another (Anderson and Hubricht 1938, Anderson 1949). Each "biological species" in Burger's oak species concept is a network of "classical" oak species that can all reproduce with one another. Burger's "biological species" is what is called a syngameon (Lotsy 1917, Dobzhansky 1937 p. 311). The term syngameon was used somewhat inconsistently in the first half of the 20th century (Dobzhansky 1937 p. 311, Hipp 2024 pp. 224–5), but it has been used from at least the 1950s onward to refer to *a group of species that interbreed but nonetheless remain distinct as species* (Grant 1971, Hardin 1975, Cannon and Lerdau 2015, Barton 2020, Buck and Flores-Rentería 2022). Syngameons are well studied in several tree groups, including pines, spruces, rhododendrons, willows, birches, and tropical trees (Thomson et al. 2015, Sun et al. 2018, Cannon and Lerdau 2019, Cannon 2021, Buck et al. 2023, Whittemore and Miller 2023, Touchette et al. 2024, Guo et al. 2025, Qin et al. n.d.). They are known across the tree of life, in clades that range from corals (Ladner and Palumbi 2012, Mao 2020), to humans (Schaefer et al. 2021, Zeberg et al. 2024) to beetles and butterflies (Boecklen 2017). Oaks are especially well-known for their syngameon behavior, in which multiple species growing together in a single stand may share alleles but remain ecologically, genomically, and morphologically recognizable (Whittemore and Schaal 1991, Dumolin-Lapegue et al. 1999 [particularly Fig. 2], Gailing and Curtu 2014, Hipp et al. 2019, Cannon and Petit 2020, Ribicoff et al. 2025, Zimmermann et al. 2025, Cavender-Bares 2025).

We are still learning how widespread syngameons are on the tree of life and what makes oak syngameons unique. What we do know is that oaks around the world have tended to evolve low to moderate reproductive barriers with relatives going back 20 million years or more, enabling hybridization and backcrossing across wide phylogenetic distances (Lepais et al. 2009, 2013, Abadie et al. 2012, Lagache et al. 2013, Eaton et al. 2015, Crowl et al. 2020, Hipp et al. 2020, Zhou et al. 2022). The resulting introgression is moderated by pollen competition, which results in reduced hybridization as numbers of individuals per species become more balanced in an oak community; and counterbalanced at least in part by ecological selection that tends to maintain species distinctions (Muller 1952, Swenson et al. 2008, Wu et al. 2024). The result is that each oak syngameon is patchy and variable on the landscape, shaped by stand-level 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. 2019, Ribicoff et al. 2025, Parker et al. n.d.).

We do not know what the relative importance of physiological barriers to breeding (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 (Servedio and Hermisson 2020, Barton 2020, 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

We have long known that oaks are distinct in habitat (Muller 1952), and that there is habitat variation both within and among groups of closely related *Quercus* species (Bourdeau 1954, Mohler 1990). Thus niche differentiation likely shapes the diversity of oak-dominated communities, as we can observe along soil, vegetation, and elevation gradients (Whittaker 1969, McCune and Cottam 1985, Spellenberg et al. 1998). Work by IOS member Jeannine Cavender-Bares beginning in the early 2000s showed that this 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, 2006, 2011, 2018).

These niche differences are the adaptations that Burger wrote about. Different oak species have evolved trade-offs between fire-tolerance and growth rate that shape niche differentiation in 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 shapes oak niche differentiation along temperature and water-availability gradients (Kaproth et al. 2023, Fontes et al. 2025). The evolution of 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) differentiates oak species along drought gradients. There are important open questions about how distantly related oak species co-occur without excluding each other competitively (Cavender-Bares et al. 2018, Cavender-Bares 2019, Hipp 2024 pp. 186–9), and we still do not know how much niche differentiation contributes to maintenance of species boundaries. But Burger's general finding 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

Oak introgression (Burger's point 1) and ecological specialization (Burger's point 2) operate in a context of high sympatric oak species diversity (Cavender-Bares et al. 2018, Cannon et al. 2024). This allows oak species to share evolutionary innovations, the "broader evolutionary advances" of their respective syngameons (Burger's point 3). Edgar Anderson argued in the 1940s that "A trickle of genes [between species] so slight as to be without any practical taxonomic result might still be many times more important than mutation in keeping up the basic variability of the parental species" (Anderson 1949 ch. 5 [esp. p. 62]). Introgression gives natural selection something novel to act on by shuttling alleles between species, influencing the evolutionary trajectory of species.

At the time that Burger was writing, it was hard to know for sure what role gene flow had on oak evolution. Cornelius Muller had hypothesized that gene flow between *Quercus gambelii* and *Q. stellata* resulted in migration of alleles from Rocky Mountains deep into eastern North America and producing *Q. margaretta* (Muller 1952 fig. 3). While this particular hypothesis has not been tested, genomic evidence shows that introgression has played an important role in European white oak migration, allowing *Q. petraea* to migrate by pollen movement and persist in colder and higher elevations due to introgression of *Q. robur* alleles (Petit et al. 2003, Leroy et al. 2020), and possibly shaping the migration of white oaks across Eurasia (McVay et al. 2017, Crowl et al. 2020). Gene flow from *Q. berberidifolia* into *Q. engelmannii* has increased genetic diversity of the latter and may have allowed the latter to adapt to the Mediterranean climate of southern California (Ortego et al. 2014, O'Donnell et al. 2021, O'Donnell 2023). Genomic data show signals of adaptive introgression between lineages in Eurasia and the southeastern U.S. (Zhou et al. 2022). Introgressed regions of the genome have been shown to be associated with climate and local conditions, suggesting an important role of introgression in adaptation (Dodd and Afzal-Rafii 2004, Nagamitsu et al. 2020, Fu et al. 2022, Liang et al. 2025).

Adaptive introgression is widespread in *Quercus*. We will still do not know how important adaptive introgression is in oaks, and studies to date are all or almost all correlative: they 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. The processes and impacts of adaptive introgression on oaks will be an area of research for decades to come. It nonetheless seems safe to say that Burger was right about the adaptive significance of oak introgression within the syngameon. Multispecies introgression has the potential to make each oak syngameon a system of populations in which numerous species contribute to each other's evolution: "more than the sum of the parts" in the words of Chuck Cannon and Rémy Petit (2020); evolution "on two fronts" in Burger's words, both the syngameon as a whole and the species that comprise it.

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Burger's view of species explicitly brings ecology into the genomic or phenotypic cluster species, supporting a view that has been articulated clearly by IOS member Alan Whittemore (1993) and James Mallet (1995): species are the clusters 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. These are the "phenotypic clusters" studied in Rieseberg's (2006) classic investigation of the nature of plant species. They are the genotypic or phenotypic clusters we use when we are researching species (Stuessy 1994, Mallet 2020). When I say "Hill's oak" (*Quercus ellipsoidalis* E.J.Hill), I don't track pollen flow in my mind; instead, I imagine individual trees that look like and grow in the same habitats and region of the globe as the other members of their classical species, discontinuous with their close relatives (Hipp et al. 2010). It is this kind of discontinuity that the researchers of the Modern Synthesis were trying to explain as they laid out a response to the question, "what is a species?" (Dobzhansky 1937, Clausen et al. 1939, Mayr 1942, Stebbins 1950). Without having access to the genome, Burger is explicit that the evolved ecological distinctions among species are their essence.

Bill Burger sent me an email in April 2019, 60 years after depositing his Master's thesis and after reading some of the new things we were finding 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 (Burger 2006, 2011, 2016). 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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