

## SPECIES DELIMITATION IN THE GENUS *QUERCUS* (FAGACEAE) DELIMITACIÓN DE ESPECIES EN EL GÉNERO *QUERCUS* (FAGACEAE)

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### Abstract

**Background:** *Quercus* is recognized as a taxonomically complex genus, but also as a model clade in many important fields in biology, such that a good recognition of its species is necessary. The chosen species concept to use in *Quercus* will determine the empirical criteria used to recognize them, which will impact several areas of knowledge.

**Questions:** What are the main sources of variation that hinder the delimitation of species in *Quercus*? What species concepts we use explicitly to recognize species in *Quercus*? What is the advantage of using different empirical criteria both integrally and simultaneously in delimitation of species of oaks?

**Studied species:** Species of *Quercus*

**Method:** Bibliographic review of the main sources of variation in *Quercus*, and the species concepts, specifically those used in *Quercus*.

**Results:** Plasticity, convergence, hybridization and introgression, and incomplete divergence were identified as the main sources of variation in oaks. Taxonomic and ecological species concepts are those mainly and traditionally used in *Quercus*. Syngameons are important to know and understand the biology and evolution of *Quercus* species. These systems indicate that there are preserved genes that provide coherence and morphologic, ecologic and genetic identity to species, even if hybridization, backcrossing and introgression occur.

**Conclusions:** Preserved genes that provide coherence to species, suggest using taxonomic, ecologic and genetic concepts to delimit problematic species in species complexes in *Quercus*. The simultaneous use of data that these concepts support (multicriteria analysis), will give more confidence to get closer to the nature of the species and build an integrative taxonomy.

**Keywords:** Criteria to delimiting species, nomenclature, species concepts, taxonomy.

### Resumen

**Antecedentes:** *Quercus* es reconocido como un género taxonómicamente complejo, pero también como un clado modelo, implicando un buen conocimiento y reconocimiento de sus especies. El concepto de especie utilizado en *Quercus* repercutirá en los criterios empíricos empleados para reconocer especies y en los resultados de su aplicación en diferentes campos.

**Preguntas:** ¿Cuáles son las principales fuentes de variación que dificultan delimitar especies en *Quercus*? ¿Cuáles conceptos de especie usamos para reconocer especies en este género? ¿Cuál es la ventaja de utilizar múltiples criterios empíricos simultáneamente para delimitar las especies de encinos?

**Especies estudiadas:** Especies de *Quercus*

**Método:** Revisión bibliográfica de las principales fuentes de variación en *Quercus* y de conceptos de especie, enfatizando en los usados en *Quercus*.

**Resultados:** Se identificó a la plasticidad, convergencia, hibridación e introgresión y divergencia incompleta como las principales fuentes de variación en encinos. Los principales conceptos de especie tradicionalmente utilizados en *Quercus* son el taxonómico y ecológico. Los singameones son importantes en el conocimiento y entendimiento de la biología y evolución de las especies de *Quercus*. Estos sistemas permiten conocer que hay genes conservados que proporcionan coherencia, así como identidad morfológica, ecológica y genética a las especies, aun cuando se presente hibridación, retrocruza e introgresión.

**Conclusiones:** Los genes que proporcionan coherencia a las especies sugieren utilizar los conceptos taxonómico, ecológico y genético en las especies problemáticas del género *Quercus*. El uso simultáneo de los datos que estos conceptos respaldan, darán más confianza para acercarnos a la naturaleza de las especies y construir una taxonomía integrativa.

**Palabras clave:** Conceptos de especie, criterios para delimitar especies, nomenclatura, taxonomía.

Species are the basic units in biological studies ([Mayer 1982](#), [Rosell et al. 2010](#), [Bacon et al. 2012](#), [Su et al. 2015](#)), and their recognition through their features, the causes and understanding of their variation are fundamental and challenging in taxonomy ([Pinheiro et al. 2018](#)). The chosen species concept will determine the criteria used for recognizing a given taxon, which will impact several aspects such as the areas of species richness, conservation and management of areas, among others ([Peterson & Navarro-Sigüenza 2001](#)).

There are many species concepts, all of them contributing to the knowledge and understanding of living organisms and their biology. However, none of these concepts is universally accepted because of issues widely discussed in previous studies ([Mayden 1997](#), [De Queiroz 2007](#), [Aldhebiani 2018](#)). [De Queiroz \(2007, 2011\)](#) highlighted that the main problem when considering a species concept unanimously lies in the fact that researchers consider the same species with different temporal perspectives, suggesting that the solution is to consider a species as separately evolving metapopulation lineages from one divergence process to the next. This criterion is a feature that the analyzed concepts have in common and was named by De Queiroz as the unified concept of species, because it arises from unifying the criteria that the analyzed concepts have in common: lineages evolving separately. Likewise, it suggests that species can be delimited through multiple lines of evidence, using for instance properties such as monophyly, reproductive isolation or diagnosability. According to [Naomi \(2011\)](#), the proposal of De Queiroz is similar to the evolutionary concept of species previously proposed by [Mayden \(1997\)](#) and considers it a synonym of this concept. The work of [De Queiroz \(2007\)](#) has the merit of emphasizing the separation of the conceptualization of species and the empirical criteria used for their delimitation.

Currently, there is a tendency to use morphologic, genetic, ecologic and geographic criteria together to define species objectively ([Ruiz-Sanchez & Sosa 2010](#), [Reeves & Richards 2011](#), [Bacon et al. 2012](#), [Su et al. 2015](#), [Pinheiro et al. 2018](#)). This has been called the multicriteria method, multiple evidence method or integrative method ([Zeng et al. 2010](#), [Bacon et al. 2012](#), [Su et al. 2015](#)). Such approaches in the delimitation of species are consistent with the proposal of [De Queiroz \(2007\)](#) of using multiple lines of evidence simultaneously, thus shedding light on this challenging task when applied to taxonomically complex groups, such as the genus *Quercus*, by giving more support and objectivity. In addition, these methods prove helpful to know and to understand their history, biology, function, and evolution.

Given their ecological, evolutionary and economic importance, oaks are widely studied and are considered as a

model in many important fields in biology such as ecology, biogeography and evolution ([Marsico et al. 2009](#), [Zeng et al. 2010](#), [Neophytou et al. 2010](#), [Torres-Miranda et al. 2011](#), [Lee et al. 2014](#), [Gutiérrez & Trejo 2014](#), [Ramírez-Toro et al. 2017](#), [Cannon & Pettit 2019](#), [Cavender-Bares 2019](#)), and a keystone in ecosystems ([Valencia-A. & Gual-Díaz 2014](#)), which is why defining and differentiating the species of the genus is fundamental.

The species of the genus *Quercus*, also known as oaks, usually present high morphological variation ([Valencia-A. 2004](#), [Nixon 2006](#), [Aldrich & Cavender-Bares 2011](#), [Sork et al. 2016](#)) and comprise several taxonomic complexes such as those studied by [Nixon & Muller \(1993\)](#), [Spellenberg & Bacon \(1996\)](#), [Romero \(2006\)](#), [Vázquez & Nixon \(2013\)](#), [Valencia-A. et al. \(2015, 2016\)](#), and [Sabás-Rosales et al. \(2017\)](#). This has resulted in treating the species concept in the genus *Quercus* in a special way ([Trelease 1924](#), [Muller 1942](#), [Burger 1975](#), [VanValen 1976](#), [Grant 1981](#), [Aldrich & Cavender-Bares 2011](#), [Simeone et al. 2013](#)).

The *a priori* recognition of species in many studies of oaks is based on the taxonomic species concept, that is, in the macroscopic and microscopic morphology in which empirical evidence requires the revision of dichotomous keys and identification of morphology in both fresh and herbarium specimens. However, given that characters evolve at different rates, using morphology alone would imply different limits than using simultaneously genetics, geography, anatomy or ecology data ([Peterson & Navarro-Sigüenza 2001](#)).

With the improvement of methods, techniques and study systems, especially in the species of *Quercus*, new evidence has emerged giving us better insight and understanding of the organization and biology of oaks, thus advancing towards a more precise recognition of its species and an integrative taxonomy. This evolution of knowledge makes it convenient to revise the concept of species in *Quercus*, which will allow greater objectivity in the delimitation of species and a supported mapping of the species among the phylogenetic relationship in the group. Therefore, the revision presented here will highlight the advantages of using different empirical criteria both integrally and simultaneously in the recognition of species of oaks, resulting in the usage of a binomial name with biological meaning. As a starting point, the possible origins of the problem in the recognition of species among oaks are highlighted, followed by the revision of species concepts used explicitly for the genus *Quercus*. It is important to clarify that neither the philosophical bases and ontology of the concepts, nor the methods used for the analysis of criteria, are discussed. For the latter topic, the study of [Sites & Marshall \(2004\)](#) is recommended.

## Results

**Problem sources.** The identification of species in a taxonomic context methodically implies the recognition of morphological features, which usually present high intraspecific variation within the genus *Quercus*, resulting in problems of species delimitation. Among the main causes of such variation are plasticity, convergence, hybridization and introgression, and incomplete divergence.

**Plasticity.** This is the response of a particular genotype to the environment or to the conditions to which an organism is subjected, determining the niche of that organism (Pigliucci 2001, Palacio-López & Rodríguez-López 2007). Plasticity can work in an adaptive way (Abrams 1994, Aldrich & Cavender-Bares 2011) and it is crucial for the persistence of long-lived species (Valladares *et al.* 2002, Ramírez-Valiente *et al.* 2010) such as oaks, increasing the fitness of individuals.

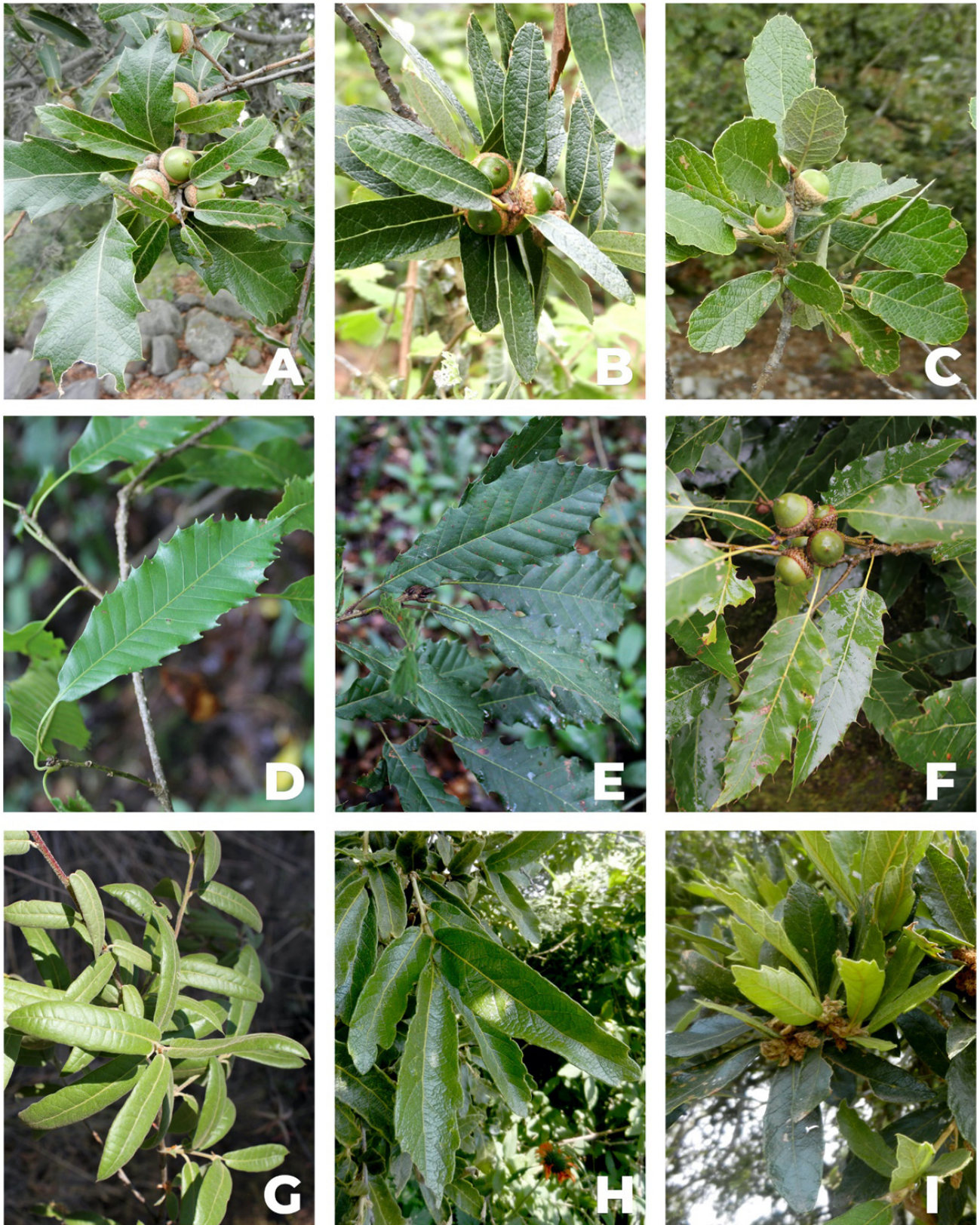
High genetic variability among species of the genus *Quercus* has resulted in an advantage by its expression, not only as chemical, physiological and developmental characters (Aldrich & Cavender-Bares 2011, Cavender-Bares & Ramírez-Valiente 2017, Ramírez-Valiente & Cavender-Bares 2017), but as morphological features as well (habit, indumentum, size, shape of leaves, buds and fruits), according to the environmental conditions in which organisms develop. Oak leaves have particularly high plastic phenotypes, leaves can present different shapes in one individual, among individuals of the same population, and in populations of the same species, such as *Q. elliptica* and *Q. castanea* (Figure 1A-1C) both species with wide distribution in Mexico; in the former Maya-García *et al.* (2020) found that the variation of the leaf length and thickness and specific leaf area are correlated with the seasonality of temperature, precipitation, elevation and aridity throughout its distribution range. Kusi & Karsai (2020) recognized that in oaks, the outer leaves with a higher exposure to sunlight are usually different (smaller and with lobules) from those that are in shade (larger and with entire margin) on the same tree, given the differences of light availability and microclimate. The plasticity among leaves coming from sprouts of most oaks differ significantly from the leaves of the rest of the tree or other individuals from the same species, leading to the determination of different species based on specimens coming from the same tree (pers. obs.). In spite of leaf variation, in classic taxonomy of *Quercus*, the main characters used for the classification and recognition are morphological leaf traits, especially shape, margin, apex, base, number of veins and indumentum; even, some studies have found that the shape of leaves, analyzed through geometric morphometric methods, could be used to delimit species and to recognize

hybrids (Fortini *et al.* 2015, Viscosi 2015, Liu *et al.* 2018, López-de Heredia *et al.* 2018, Albarrán-Lara *et al.* 2019).

**Convergence.** Plants that are systematically distant can present certain morphological similarities (Font-Quer 1963), usually from growing in similar environmental conditions. Numerous cases of convergence in leaf morphology of oaks have been studied, such as *Quercus costaricensis* and *Q. bumelioides* both from montane rain forest at Cordillera de Talamanca, in Costa Rica, which can be confused due to the shape of the leaves, despite belonging to different sections (Nixon 2006, Hipp *et al.* 2018, Rodríguez-Correa *et al.* 2018). Another similar case is that of *Q. meavei*, *Q. paxtalensis* and *Q. corrugata* with a similar shape of the leaves (Figure 1D-F), and also from montane rain forest but in Mexico. *Q. crassipes* and *Q. deserticola* could be confused with *Q. castanea* since its leaves can be indistinguishable in similar environmental conditions, do not matter belong to different sections (Figure 1G-I). Some shrubby white oak species of California that grow in dry habitat, open chaparral and in close geographical proximity, are similar in the size of leaves, texture, and margin (with spiny) (Nixon & Muller 1997, Ortego *et al.* 2017). Likewise, shrubby species from semi-arid regions in northeastern Mexico present morphological convergence in several leaf features (Sabás-Rosales *et al.* 2017). Some physiological convergences for oaks have also been studied, Cavender-Bares (2019) points out phenotypic similarities and convergences in characters related to the adaptation to fire, humidity and soil fertility in different lineages of oaks that share the same habitat. The presence of annual fruits in different lineages of the section *Lobatae* is a convergence of some species that thrive in warm-humid locations in southern Mexico and Central America (Nixon 2006), but also this character is present in sections *Cyclobalanopsis*, *Cerris*, *Ilex*, *Quercus*, *Virentes*, and *Ponticae*. Convergent transitions in the amount of leaf retention in oak species (deciduous, briefly deciduous, evergreen) are shown as a response to similar biogeography, climate, and soils (Hipp *et al.* 2018). Convergences can lead to incorrect determination of species and misinterpretation in the evolution of characters.

**Hybridization and introgression.** Hybridization is defined as the reproduction of members of genetically different populations (Barton & Hewitt 1985) and introgression is defined as the incorporation or infiltration of alleles from one species into the gene pool of another species, through hybridization and backcrossing (Anderson 1949, Harrison & Larson 2014). Both processes occur randomly and spontaneously among many species of the same section of the genus *Quercus*. These events are usually favored by environmental disturbances (Ortego *et al.* 2017) and they

oak species delimitation



**Figure 1.** A-C. Variation in the shape of *Quercus castanea* leaves. D. *Quercus corrugata*, E. *Q. meavei* and F. *Q. paxtalensis*, the last three with similar shape of leaves, and living in montane rain forest. G. Leaves of *Quercus crassipes*, notice the similarity of leaves with that in picture 1B of *Q. castanea*. G, H. Variation in the shape of *Q. deserticola* leaves, notice the similarity with that of *Q. castanea*.

function as a source of innovation that produces quick adaptations that are useful to face environmental changes (Rieseberg 1997, Abbot *et al.* 2013, Cannon & Petit 2019) and to introduce advantageous mutations in a different genetic pool (Leroy *et al.* 2017).

Hybridization and introgression are processes studied in extant species, but McVay *et al.* (2017) said that there are ancient introgression events that could have occurred between extinct species or those that are no longer sympatric, such as the ancestors of *Ponticae* and *Roburoid* lineages. Suggesting that these processes have played an important evolutionary role in oaks.

Studies on oak hybridization and introgression are generally carried out in two-species systems, however in the last decade, some analyses have identified three- to six-species systems with gene flow in American oaks (Dodd & Afzal-Raffii 2004, Peñaloza-Ramírez *et al.* 2010, Zhang *et al.* 2015, Sullivan *et al.* 2016, Castillo-Mendoza *et al.* 2018).

Given the interspecific genetic flow, it is common to find individuals with unusual, intermediate or transgressive features suggesting a possible hybrid or backcrossing origin. These individuals might be important in the evolutionary processes within the group, as they work as bridges in the genetic flow of information from one species to another, thus increasing the genetic diversity of the receiver species and possibly originating preadaptations that would allow the occupation of different niches. Despite these evolutionary advantages, the genetic flow among individuals from different species counters the established biological species concept (Mayr 1999) and is considered as the worst scenario to exemplify this concept (Coyne & Orr 2004). This is also the case for the taxonomic species concept, as there are novel morphological variations in hybrids, including intermediate or transgressive variation (Rieseberg *et al.* 1999), that are problematic when trying to locate these individuals in a classification system. Although hybrids can be formally named as the International Code of Nomenclature for algae, fungi and plants (Turland *et al.* 2018) point out, I consider that formally naming each case can be an endless task that would complicate communication in biology.

*Incomplete divergence.* At the end of the lineage divergence process, some features become clearly distinguishable among the divergent lineages, gametes and breeding systems become incompatible and the lineages colonize different habitats (De Queiroz 2007). But while the lineages are diverging, their characters undergo several evolutionary states, because the divergence is a gradual process that starts with the incipient segregation of populations until their complete separation, without order and asynchrony in the evolution of their properties. The genus *Quercus* comprises

species that diverged recently (Hipp *et al.* 2018, 2020). In the American tropics, the regions with most diversity, it has been proposed that divergence of extant species started approximately 10 million years ago, in the second half of the Miocene and extending towards the Pliocene (Hipp *et al.* 2018, 2020), although for some other tropical species of the section *Virentes*, divergence could be more recent (Gugger & Cavender-Bares 2013, Cavender-Bares *et al.* 2015). The divergence of the genus *Quercus* is related to a rapid evolution caused by preadaptive genetic variation, and availability of different habitats to colonize (Hipp *et al.* 2018, Cavender-Bares 2019), producing isolated populations that diverge due to their flourishing in different environments. Relatively recent divergence can present weak reproductive barriers and hybridization may still be possible, as in many cases of oaks. An incomplete or recent divergence can make some of the attributes not entirely discrete, making species recognition more difficult, as the case of *Q. magnoliifolia* and *Q. resinosa* with recent divergence (Hipp *et al.* 2020), and which show morphological and ecological differentiation from each other, but low levels of genetic differentiation (Albarrán-Lara *et al.* 2019).

*Concepts of species used in Quercus.* Among the first investigators who used explicitly the taxonomic concept in the genus *Quercus* are Trelease (1924) and Muller (1942). They recognized the taxonomic species concept based on phenetic discrete and separated units due to the discontinuity in the variation (Stace 1978). Muller (1942) had problems when deciding whether a recognized group represents a species or variety (the level given), not the identification of discontinuities and groups themselves. The hierarchical level given to taxonomic groups has been controversial throughout the history of taxonomy, including sometimes phylogenies of big groups (Mishler & De Luna 1997). Muller (1942) uses a broader species concept than Trelease, as he considers varieties, forms and some species described by Trelease as simple variations of species.

Grant (1971), Burger (1975) and Hardin (1975) questioned the usage of the biological species concept in oaks, due to the frequent hybridization between different species. They highlighted that this concept could imply a complex system of crossing populations called syngameon, a group of species that present interspecific genetic flow under changing environmental conditions, but with each species preserving their morphological integrity (Cannon & Petit 2019), thus allowing its recognition as a taxonomic species.

Aldrich & Cavender-Bares (2011) mentioned that their studies are based on the concept of Wittgenstein published in 1958, which considers a group or set of characters to recognize species, and that are not necessarily at the same

level (morphologic or genetic). [Simeone et al. \(2013\)](#) considered that in order to define the identity of the species of *Quercus*, it is necessary to make a thorough revision based on the synergy of multiple data for each taxon, such as ecology, morphology, history and genetics.

On the other hand, based on the variation observed in species of *Quercus* and the lack of reproductive isolation in some of them, [VanValen \(1976\)](#) highlighted that species should be recognized by the adaptive zone used, and should also present minimum differences from other lineages and evolve separately from all the lineages. The adaptive zone is considered by [Anderson \(1990\)](#) as a similar concept to the ecological niche, which could be recognized through ecological criteria; and niche could be “a term describing the role of a species or population in its ecosystem” ([Martínez-Gordillo et al. 2009](#)).

Although there could be speciation without ecological divergence in oaks ([Cavender-Bares 2015](#)), [Hipp et al. \(2018\)](#) show that the niche diversification has driven the high diversification in Mexican oaks. Although the environmental or ecological data are little known or difficult to quantify for some species, ecological niche modeling helps to define the main climatic conditions where the species are present (e.g., [Martínez-Gordillo et al. 2009](#), [Ramírez-Preciado et al. 2019](#), [Song et al. 2019](#)). These models have their basis on the relationships between the distribution of a species and its environmental conditions ([Booth et al. 2013](#)). Additionally there are several studies on traits related to ecological functional such as leaf size ([Cavender-Bares et al. 2015](#), [Maya-García et al. 2020](#)), height of plant ([Cavender-Bares et al. 2015](#)), leaf habit ([Hipp et al. 2018](#)), hydraulic capacity ([Arenas-Navarro et al. 2020](#)) that are linked to niche differentiation in oaks, and are important in local adaptation ([Dagnino et al. 2017](#)). These traits together with reproductive isolation can lead to speciation, and show the importance of the ecological niche as part of this process and with the identity of the species, and suggesting that the ecological pattern could be useful to enable the recognition of species limits as the Ecological Species Concept points out ([VanValen 1976](#)).

*The concept of species and binomial nomenclature.* Species are considered as evolutionary, ecological, working and communication units, and to consider them as such they must be consistent with what the names represent and allow the organization of knowledge and the retrieval of a functional information system ([Trelease 1924](#), [Burger 1975](#)).

Scientific names represent systems with biological significance ([Burger 1975](#)). The name is important because it is key in accessing knowledge generated in the referred group, and it symbolizes large amounts of knowledge and comprehension of the group. In this way, it is noteworthy to

say that adequate knowledge and information from various sources and levels are then required to assign a name. These sources of information should explain different characteristics of the species in order to delimit, understand them, and thus, translate them easily to morphological features for practical recognition.

*Concepts and useful criteria in the recognition of Quercus.* In the conceptualization or ontology of the species, the unified species concept proposed by De Queiroz is suitable when considering that species of *Quercus* are lineages with an origin and destiny, including genetic, morphologic, ecologic, physiologic, chemical and reproductive attributes (and others) that have been developed at different rates throughout history. The phylogeny of American oaks ([Hipp et al. 2018](#)) shows species both close to and far from the point of divergence, suggesting different times of origin, which means that species have evolved at different rates with differences in the development of their features.

The previously described concepts for the study of oaks are operational concepts based on the recognition of species mainly through morphological, genetic or ecological features, and that can be visualized as relevant lines of evidence used for delimit species.

If these could be applied simultaneously, they could be a reliable tool to approach the true limits of the species.

An important attribute in the evolution of oaks that should definitely be taken into account is to consider species as part of a syngameon or interspecific reproductive net, where species are undifferentiated even where genetic flow exists through hybridization, backcrossing and introgression ([Cannon & Petit 2019](#)). Belonging to a syngameon confers the opportunity to enhance genetic diversity, and thus preadaptive advantages towards new niches. [Cannon & Petit \(2019\)](#) published: “The oak syngameon: more than the sum of its parts” and emphasized the potential advantages of belonging to a syngameon, as this is a source system of novelties, genetic diversity, rapid adaptation and high plasticity for all member species, which co-evolve as a whole.

The study of syngameons has allowed us to know and understand better the variation, evolution, reproduction and consequently the biology of species of *Quercus*, and also that, even though there are events of hybridization and introgression, it is possible to recognize species in *Quercus*. According to [Hipp et al. \(2019\)](#), during events of hybridization and introgression the complete genome is not always recombined, as some regions may be kept isolated, giving coherence to these species as well as morphological, ecological and genetic identity ([Burger 1975](#), [Williams et al. 2001](#), [Lepais et al. 2009](#), [Zeng et al. 2010](#), [Valencia-Cuevas et al. 2014](#), [Gailing & Curtu 2014](#), [Eaton et al. 2015](#), [Ortego](#)

*et al.* 2017, Leroy *et al.* 2017). According to Leroy *et al.* (2020), genetic differentiation at species level is restricted to a few genes that give uniform morphology for the recognition of a species, and these may be related to preserved genes corresponding to ecological tolerance to drought, cold and saline soils, and other genes related to biotic interactions and intrinsic barriers, phenology, pollen recognition and growth. The rest of the genetic information seems to be shared among the species of the syngameon (Muir & Schlöterer 2005, Curtu *et al.* 2007, Neophytou *et al.* 2010, Leroy *et al.* 2017).

## Conclusions

When considering the preserved genes mentioned earlier that provide coherence and morphologic, ecologic and genetic identity, the relevance of using the taxonomic, ecologic and genetic concepts (evolutionary or phylogenetic) is evident. We can take as a starting point the taxonomic concept as the most practical, and in many cases being sufficient, but in other more complex groups it is recommended to include criteria used to define species from all three concepts, that is, multicriteria studies. Conceptually speaking, the unified concept proposed by De Queiroz provides a good frame of reference.

Multicriteria studies are used not only to define the limits, variation and hybridization of species of *Quercus* as in *Q. laurina* and *Q. affinis* (González-Rodríguez *et al.* 2004), *Q. magnoliifolia* and *Q. resinosa* (Albarrán-Lara *et al.* 2019); but also to show the evolution of oak species, for example in Section *Virentes* (Cavender-Bares *et al.* 2015), *Q. chrysolepis* (Ortego *et al.* 2015), Series *Agrifoliae* (Duncan *et al.* 2017), Subsection *Racemiflorae* (McCauley *et al.* 2019), and *Q. elliptica* (Maya-García *et al.* 2020).

Defining and delimiting species of the genus *Quercus* remains a challenge in many complexes such as *Acutifoliae*, *Microphylla*, *Crassifoliae* and *Rugosae* (among others). However, breakthroughs in multiple fields of knowledge will allow better understanding of their evolution and biology, with likely positive effects on taxonomy, phylogeny, and conservation.

The multiple species concepts and their usage along with empirical data provide different kinds of information that should all be considered consistent and practical, both simultaneously and integrally, so that species can be recognized. The coexistence of different compatible species concepts for a group and the use of empirical data coming from different levels or sources, will provide further confidence regarding the nature of species (Sangster 2018), contributing to the knowledge and understanding of their biology.

The taxonomic complexity of *Quercus* and its consideration as a model clade, will promote the discovery

of a great deal of new information, and possible changes in the delimitation and recognition of some species and their nomenclature. However, such changes do not correspond to the artificial creation of limits, but to the discovery of new information supporting a robust and integrative taxonomy, with more objective analysis, and which can be considered as the starting point for many other studies. After obtaining new knowledge in different study areas, it is probable that it will be necessary to review the limits of species for adjustments or modifications. Finally, species and their boundaries stand as a refutable hypothesis that is intended to have a better approach to reality based on current knowledge (Raposo *et al.* 2017, Sangster 2018).

The recognition and delimitation of species of oaks is challenging, but the possibility to know and understand the processes that intervene in their biology through the integral application of multiple criteria and different species concepts will enhance confidence when recognizing, delimiting and renaming species with biological significance. A better understanding of the biology of the species will affect their delimitation and taxonomy, resulting in a positive impact in different studies carried out on *Quercus* species.

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