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Mini Review

Revisiting the Axelrod's Hypothesis: What is the Origin of the Evergreen Sclerophyllous Oaks in the Northern Hemisphere?

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Abstract

Axelrod proposed a hypothesis to explain the origin and evolution of the evergreen sclerophyllous flora in the Northern Hemisphere, suggesting an *insitu* differentiation of clades at low-mid latitudes during the Cenozoic. This hypothesis highlights a continuous belt of sclerophyllous vegetation that was fragmented over time due to tectonic movements and climatic changes, including cooling and drying. The genus *Quercus* exhibits numerous sclerophyllous species, which reach their highest diversity in the latitudes he identified. However, the evolutionary histories of the two subgenera within *Quercus*-the New World and Old-World clades-show distinct patterns. This review examines whether Axelrod's hypothesis holds true for *Quercus* by synthesizing recent molecular phylogenies, fossil records, and biogeographic analyses. Findings reveal that while Old World oaks largely align with Axelrod's hypothesis, the recent diversification of the tropical New-World oaks challenge the framework he proposed.

Introduction

Genus *Quercus* (oaks) is the most biodiverse genus within the Fagaceae family, comprising more than 400 species distributed across the Northern Hemisphere. Oak species, together with pines, play a critically important role in forest ecosystems, as they account for the largest arboreal biomass and support the greatest species diversity within mid-latitude forests [1]. Unlike other genera, like the a for mentioned *Pinus* or the closely related *Lithocarpus*, oaks display significant variability in the morphological, anatomical, phenological, physiological and ecological traits and strategies. This heterogeneity has allowed oak species to occupy a wide range of different climates and environments across the vast distribution range of the genus [2]. The exact number of oak species remains uncertain and is likely to remain so indefinitely. The difficulty lies in the remarkable plasticity of the morphological traits of these species, as well as in hybridization and introgression among species. Nonetheless, several authors committed with this genus have recently solved many relationships within the infrageneric clades-which have undergone extensive reclassification through time-by applying molecular data [3-8]. Thus, after the last major revision of the subgeneric clades [5], the genus *Quercus* has been classified into two subgenera: subgenus *Cerris* (Old World oaks) and subgenus *Quercus* (New World oaks), and eight sections: *Cyclobalanopsis*, *Ilex* and *Cerris* for subgenus *Cerris*, and *Lobatae*, *Protobalanus*, *Ponticae*, *Virentes* and *Quercus* for subgenus *Quercus* (Figure 1). Every section is currently present strictly in its respective part of the world except for Sect. *Quercus*, which has a Holarctic distribution and the two disjunct species of Sect. *Ponticae*. Although studies before 2017 were considering some different conceptions of the sections or subgenera, we will be referring to the current ones in this review. The origin of both subgenera is believed to lie in their respective regions, the Old World [8] and the

New World [9]. The connection of both subgenera and, therefore, the center of origin for the whole genus remains unknown. It could have originated in North America, in Asia (as the rest of the Fagaceae genera) or the common ancestor could have a widespread circumpacific distribution [10]. Biogeographically, oak species are present in four realms: Nearctic, Neotropical, Palearctic and Indomalayan. However, given the current distribution and the evolutionary history, it is more practical to consider three broad regions: The Americas, Eastern Asia and Europe (including North Africa and the westernmost part of Asia) (Figure 2). The Americas account for more than half of the species in the genus (~220 spp.), being Mexico the hotspot of biodiversity (~150 spp.) [11,12]. Eastern Asia (~140 spp.), and specially China, represent the most diverse area for oaks in the Old World. Finally, Europe has a few more than 30 oak species, with the Mediterranean basin accounting for the most biodiversity. The current distribution of the different species and clades becomes more intriguing when the evolutionary history of the different lineages is considered.

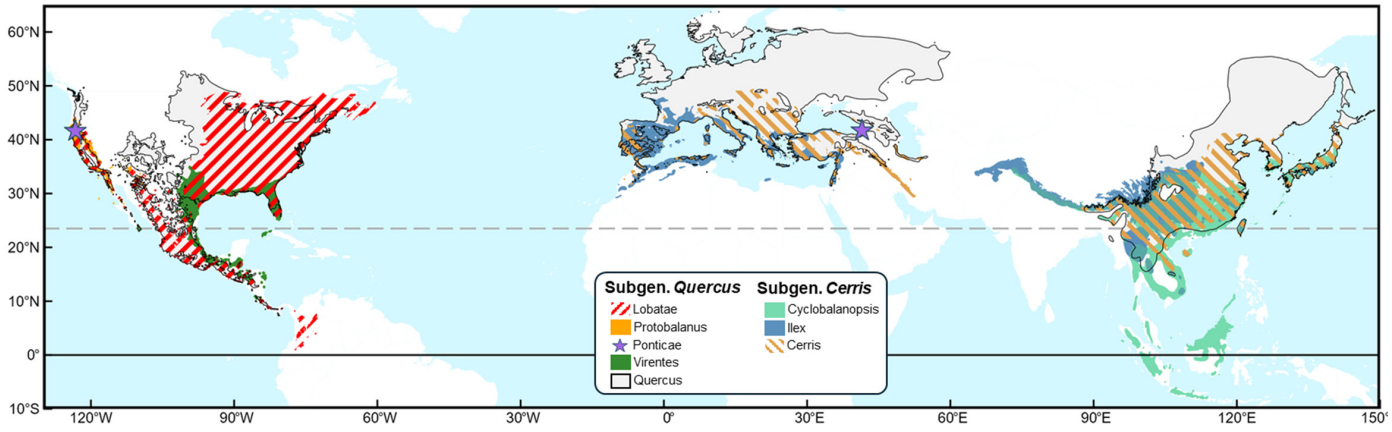

Figure 1: Current distribution of the eight sections within genus *Quercus*.

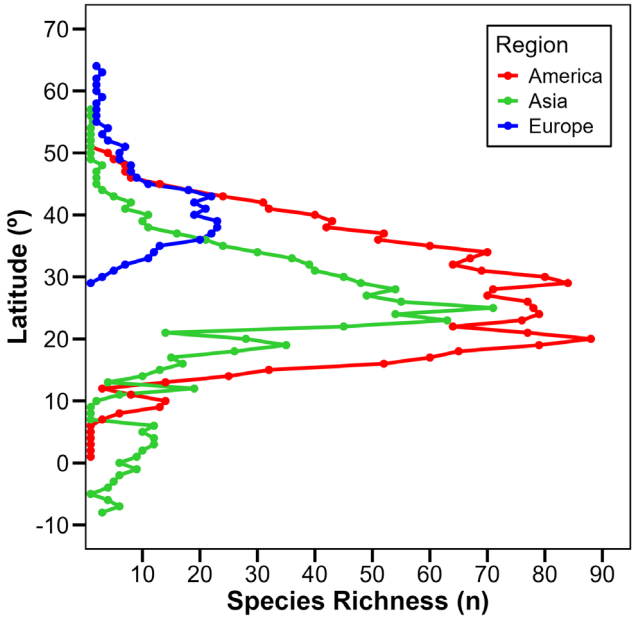

Figure 2: Species richness (n=number of species) across the latitudinal gradient of the three current broad areas of *Quercus* presence.

Axelrod's hypothesis

Daniel I. Axelrod introduced a hypothesis in 1975 to explain the origin of the evergreen sclerophyllous flora in the Northern Hemisphere. He proposed the presence of a continuous belt of sclerophyllous vegetation-represented by numerous taxa-occupying low-middle latitudes (around 30ºN, see Figure 1 in his original work) in the Late Cretaceous, when these ancestors lived under warm temperate to subtropical climate conditions. Note that Europe was further south at that time, and North America, to a lesser extent, as well. This ecotone would have been composed

for taxa of both temperate and moist-tropical sources, primarily the latter. Sclerophyllous trees and shrubs would have originated in such areas at the beginning of the Cenozoic, resembling their close living relatives. This continuous belt would have been fragmented due to both the separation of continents for tectonic movements and the drastic climatic changes through the Cenozoic, this is, cooling and drying, which would have created some areas (grasslands, steppes and deserts) presently too dry for these species. Thus, species sharing this evolutionary history would form the so-called Madrean-Tethyan disjunction, alluding to the Sierra Madre in Mexico and the Tethys Sea in Eurasia, respectively. Since the ancient taxa-living under relatively warm and moderately mesic conditions-already presented several xeromorphic traits, and they resemble the modern species, Axelrod suggests a preadaptation of such taxa to dry conditions. In this sense, he defines sclerophyllous vegetation as generalist rather than specialist, contrary to many ecologists. The main reason lies on the fact that sclerophyllous taxa can be found in very different ecosystems. This also applies to oaks, which gather a great gradient of sclerophylly (traditionally related to Leaf Mass per Area, LMA) [13,14]. The most sclerophyllous oak species can be found in Mediterranean-type and arid climates (see Q. *chrysolepis* in California or *Q. rotundifolia* in Spain). However, somewhat sclerophyllous species can be found in the other ecosystems exposed by Axelrod for this flora:

a) Montane forests, with summer rain (see *Q. sebifera* in eastern Mexico or *Q. franchetii* in Hengduan Mountains)

b) evergreen scrub at timberline (see *Q. semecarpifolia* or *Q. monimotricha* in the Himalayas) and

c) ever-wet tropical rainforest (see *Q. insignis* or *Q. costaricensis* in Mesoamerica).

All these sclerophyllous species typically occur at low-middle latitudes, which match either with the highest diversity within the genus (Figure 2) or with the latitudes proposed by Axelrod to be their origin. Finally, numerous malacophyllous deciduous oak species significantly contribute to temperate broadleaf and mixed forests, which would trace their origins to the Arcto-Tertiary flora.

"The relations suggest that in the Tethyan and Madrean regions semihumid sclerophyllous vegetation

a) has formed an ecotone between tropical and temperate forests throughout its history,

b) that it derived taxa from both sources, though chiefly the former,

c) that it had a wider distribution in the past, covering areas presently too dry for it,

d) that the present restricted distributions reflect selection and segregation in response to the development of new dry climates during the Quaternary" [12].

Once Axelrod's hypothesis has been exposed and the genus *Quercus* is among the taxa that were originally considered to follow this hypothesis, the main question addressed is: according to the studies carried out from 1975 to today, do oaks still follow this hypothesis in both the New and Old World?

The new world

Trelease (1924) was among the first authors to suggest an origin for American oak species in his extensive work. He proposed a primary center of distribution in what is now Arizona from a single primitive ancestor resembling the extant *Q. chrysolepis*. From there, oaks would have migrated to west (California), east (Eastern USA) and south (Mexico). This agrees with Axelrod's hypothesis proposed fifty-one years later. Manos [15] by using ITS and chloroplastic DNA in their in-depth study of Sect. *Protobalanus*-show how *Protobalanus* is a monophyletic section within the New World clade (currently Subgenus *Quercus*) and they suggest that the resemblance of these species with holly oaks (Sect. *Ilex*) is the result of homoplasy. In short, they cast doubt on Axelrod's belt of sclerophyllous taxa being composed of monophyletic clades within the genera. However, they are not denying the hypothesis, since they defend an *in-situ* speciation for the *Protobalanus* clade. Two years later, Manos and Stanford [10] again support the Axelrod hypothesis by claiming that all major oak lineages essentially evolved in the areas where they occur today (see Figure 8.5 in [16]) for a graphical support to these conceptions). A second equally important conclusion drawn from [15] is that the origin of all current New World sections is located in the Americas. Californian floristic province can be taken as a useful reference for a complex assemblage of temperate, subtropical (madrean), and desert elements [17,18] with numerous sclerophyllous taxa, including oaks. Ackerly [18] shows how most of the taxa studied in his paper-any *Quercus*-presented a cool temperate origin, although he still finds two taxa (*Prunus subgen*. *Laurocerasus* and *Rhus*) with traces to tropical origins. It might be considered as a first suggestion that the sclerophyllous flora in North America could have a significant contribution from temperate ancestors. In 2018, the first comprehensive and groundbreaking phylogeny of the New World oaks [9] revealed remarkable conclusions [19]:

a) the common ancestor of every species of subgenus *Quercus*-including Sect. *Quercus*-is in North America, agreeing with [15].

b) however, the common ancestor would have a temperate origin, supporting Ackerly [18] and confronting both Manos [15] and Axelrod [12].

These conclusions will be recovered again by *Cavender-Bares* [3] in her Tansley review. Months later, the global phylogeny of oaks was updated, including many Mexican and Old-World species [7]. In this paper, a Miocene origin of the Mexican clades for both red and white oaks is supported, becoming Mexican oaks the most recent lineages in the genus. Species in Mexico and Mesoamerica are represented by numerous broad-leaved, evergreen or brevideciduous, sclerophyllous species, but the recent colonization of these areas is incompatible with the hypothesis proposed by Axelrod, who proposed a Paleogene *in-situ* differentiation of the sclerophyllous taxa.

The old world

It is well known that the present European vegetation is composed mainly of two separate ecological units: the evergreen, laurophyllous "Palaeotropical geoflora" and the deciduous, broad-leaved "Arcto-Tertiary geoflora" [20,21]. At the beginning of the Cenozoic, the southernmost region of Europe consisted of an extensive archipelago in the Tethys Sea, located significantly farther south than its current position. This latitude, combined with the climatic conditions of the time, defined a warm temperate to tropical climate across the entire archipelago. Several palaeotropical taxa with a widespread distribution during the Tertiary in these subtropical areas are currently present as relict flora in several refugia (see *Rhododendron ponticum*, *Ilex aquifolium* or *Prunus lusitanica*, for example) [22,23]. Concerning oaks, there has been a debate about whether they originated in Europe and migrated to Asia, or vice versa, driven by the diverse fossil records of pollen, acorns and leaves across the Old World throughout the Cenozoic [24]. However, three independent studies with molecular analyses have revealed an Asian origin during the Oligocene for the three sections *Cyclobalanopsis* [4], *Ilex* [6] and *Cerris* [8], followed by a rapid diversification until the Miocene. The exact latitude of the center of origin for each section slightly varies depending on the study, from a warm temperate (Sect. *Cerris*) to tropical (Sect. *Cyclobalanopsis*). Nonetheless, the common ancestor of all Old-World oaks can be attributed to Palaeotropical areas in Eastern Asia, supporting Axelrod's hypothesis. After an initial radiation, both Sect. *Cerris* and *Ilex* migrated westwards to reach Europe. Section *Cerris* migrated to Western Eurasia north of the progressively enlarging Qinghai-Tibet Plateau whereas Sect. *Ilex* migrated south of the Qinghai-Tibet Plateau, following the proto-Himalayas [6,8]. Unequivocal fossil records of sclerophyllous oaks in Western Eurasia can be found in the late Miocene, represented by the fossil complexes *Q. drymeja* and *Q. mediterranea* [5]. Although the Miocene cooling had already started by then, the Mediterranean climate was not established until Pliocene (ca. 3.2 Ma ago) [25]. Since Sect. *Ilex* has been morphologically quite homogeneous since its origin, characterized by evergreen habit, sclerophyllous leaves, and xeromorphic traits, it is reasonable to assume that ancient taxa were pre-adapted to the emerging Mediterranean conditions, a postulate also proposed by Axelrod [12].

Conclusion

Although the origin of the genus is still unknown, the evolutionary histories of the both subgenera are better understood. New World oaks present a temperate, mid-latitude origin (Arcto-Tertiary), with a colonization and speciation occurring progressively from north to south, eventually reaching Mesoamerica in recent times. Consequently, the evergreen sclerophyllous oaks found in Mexico and Mesoamerica did not arise from the continuous belt of sclerophyllous vegetation proposed by Axelrod, thereby refuting his hypothesis. In contrast, evergreen Old-World oaks have a warm-temperate origin in Eastern Asia (Palaeotropical), aligning with the latitudes proposed by Axelrod. Subsequently, these oaks migrated westwards into Europe, following the continuous belt of sclerophyllous vegetation, and eventually reached the subtropical Mediterranean basin of that time, supporting Axelrod's hypothesis. In summary, while Axelrod's hypothesis cannot be applied to the genus as a whole, it remains valid for Old World oaks but has been disproven for New World oaks.

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