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Oaks (*Quercus* spp.): A Brief History

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Quercus (oak) is the largest tree genus in temperate and sub-tropical areas of the Northern Hemisphere with an extensive distribution. (Denk et.al. 2010) Oaks are the most dominant trees of North America both in species number and biomass. (Hipp et.al. 2018) The three North America oak groups (white, red / black, and golden-cup) represent roughly 60% (~255) of the ~435 species within the *Quercus* genus worldwide. (Hipp et.al. 2018; McVay et.al. 2017a) Oak group development over time helped determine current species, and can suggest relationships which foster hybridization.

The red / black and white oaks developed during a warm phase in global climate at high latitudes in what today is the boreal forest zone. From this northern location, both oak groups spread together southward across the continent splitting into a large eastern United States pathway, and much smaller western and far western paths. Both species groups spread into the eastern United States, then southward, and continued into Mexico and Central America as far as Columbia. (Hipp et.al. 2018) Today, Mexico is considered the world center of oak diversity. (Hipp et.al. 2018) Figure 1 shows genus, sub-genus and sections of *Quercus* (oak).

History of Oak Species Groups

Oaks developed under much different climates and environments than today. By examining how oaks developed and diversified into small, closely related groups, the native set of Georgia oak species can be better appreciated and understood in how they are related, share gene sets, or hybridize. Oaks have migrated widely, driven by climatic change, especially under changing temperature, precipitation, edaphic (soil) and climatic variability or disturbance. Across time, oaks have adapted to and thrived under local weather and topographic conditions, as well as interference (competition + allelopathy) from other oak species and other forest / woodland trees. Oaks have continued to adapt and diversify under geographic isolation – in valleys and plains, along ridges and coasts, and scattered across mountain ranges.

The beginnings of what would become the oaks can be traced in the fossil record back more than a 100 million years ago (i.e. 100mya). There has been much gene flow and exchange of tree families and species between continents and across the Northern Hemisphere over the last 150 million years, or since the beginning of the Cretaceous. Figure 2 defines the geologic time periods used here. North America and Iberia (Spain / Portugal area) were connected around 154mya, and North America and Northern Europe were connected 131mya. (Brikiatis 2016). The rise of *Angiosperm* trees occurred when there was much interconnection of landmasses with the Northern Hemisphere.

Land Bridges

In addition to early large continental connections, North America has experienced five ephemeral connections with other landmasses over the last 100 million years. Oaks migrated over both the Beringia (Bering Sea) and North Atlantic land bridges, spreading widely. These connections occurred in the Paleocene (61mya), Eocene (45mya), Oligocene (28mya – Beringia only), Miocene (15mya), and Pliocene (5.3mya). (Graham 2018)

Many tree species groups of North America arose during the 110mya to 80mya time period leading to our modern tree families and species. The beech family (*Fagaceae*), and predecessors of oaks (*Quercus*), have been recognizable since around 100mya. The beech family developed in Asia and migrated back and forth across Beringia. (Manos & Stanford 2001)

The modern represenatives of the beech family are shown in Figure 3. The beech family is currently listed with ten genera and about 925 species. (Manos et.al. 2001) The *Quercus* genus developed as a North American split from Asiatic beech family groups, eventually dispersing further to Eurasia over the North American land bridges. (Manos & Stanford 2001)

Mountain & Oak Rise

Just after the rise of the Rocky Mountains between 80-55mya, divergence of old and new world oaks began around 55mya in the northern areas of the Northern Hemisphere. (Hipp et.al. 2018; Hubert et.al. 2014; Manos & Stanford 2001) The modern oak genus is considered to have been established in the high latitudes of North America, around the Paleocene-Eocene time boundary (56mya). (Hipp et.al. 2018; Hubert et.al. 2014). The climate at this time was very warm with atmospheric carbon-dioxide at twice today's levels.

By 45mya, the old world oaks were diverging into the cycle-cup oaks (*Cyclobalanopsis*) and the *Ilex / Cerris* oak groups. (Hubert et.al. 2014) The new world high latitude oaks started to radiate and diversify southward across North America by 35mya. (Cavender-Bares et.al. 2018) Figure 4. Global temperatures decreased ~8°F around 34mya and oaks were pushed further southward. (Hipp et.al. 2018)

Southward

As oaks were forced south, this was a time of divergence between the new world red / black oak group *(Lobatae)*, and the white / golden-cup oaks *(Quercus / Protobalanus)* (34mya). (Hipp et.al. 2018; Hubert et.al. 2014) Although some researchers have placed this divergence later at 28 mya. (Hipp et.al. 2014) Both white oaks in general, and the *Roburoids* (Eurasian white oaks) specifically, were of New World origins with multiple movements and exchanges into Eurasia. (Crowl et.al. 2019; McVay et.al. 2017a)

Around 33-34mya the Californian, Eastern United States, Eurasian, and Northern Mexico white oak groups began to develop and separate. (Hipp et.al. 2018) Red / black, white, and golden cup oak group were present by 30mya. (Cavender-Bares et.al. 2018) The golden-cup oaks (*Protobalanus*) separated from the white oaks roughly 25mya and were widely distributed across all of North America in the Paleogene (23-25 mya). (Denk et.al. 2017; Hipp et.al. 2018) Some researchers place this divergence much later (i.e. 15mya). (Hubert et.al. 2014) The *Roburoids* (Eurasian white oaks) also split from Eastern North American white oaks by 25mya. (Denk et.al. 2017) The predecessors of the *Roburoids* migrated a number of times across the North Atlantic land bridges. (Crowl et.al. 2019)

Diversify

By the end of the Paleogene / start of the Neogene (23mya), wide-spread radiation and diversification of white oaks across North America and the rest of the Northern Hemisphere had occurred. (Denk et.al. 2017) Red / black and white oaks together had widely colonized both eastern and western North America by 20mya. (Cavender-Bares et.al. 2018) A period of rapid diversification of oaks occurred between 18mya and 12mya, leading to more Eurasian white oaks, Mexican / Texas white oaks, United States southwest white oaks, and Mexican red oaks. (Hipp et.al. 2018) The Mexican and Central American oaks diversified at roughly twice the rate of the rest of North American oaks between 16mya to 10mya. (Hipp et.al. 2018)

Old world oaks underwent a divergence period around 18mya between the *Ilex* and *Cerris* oak groups. (Hubert et.al. 2014) By the middle Miocene (15mya) white oaks covered North America from mid-latitudes to arctic regions. (Denk et.al. 2010) As Sierran (15-10mya) and Cascade (17-15mya) mountains were thrust up, populations of some far western oaks were isolated. Diversification of far western red oaks (*Quercus* section *Lobatae* series *Agrifoliae*) occurred around 15mya. This was a period of changing climate with increasing warming and aridity. (Hauser et.al. 2017)

A number of oak species have remained unchanged since the Miocene (15mya), especially in temperate zones. (Petit et.al. 2003) Between 15mya and 11mya in the Eastern United States, southern live oaks evolved, although some authors place this development much farther back in time (i.e. 30mya). (Hipp et.al. 2018; McVay et.al. 2017a) Figure 5.

Last Colonist

Gene flow between New World white oaks and Old World white oaks had been occurring relatively often until 5.5mya across North Atlantic land bridges, and the Beringia land bridge. (Hubert et.al. 2014) North American deciduous red and white oaks had crossed a North Atlantic land bridge around 8-9mya (under a warm climate), and again around 5.5-6mya (under a cool climate). (Denk et.al. 2010; Denk et.al. 2017) Eurasian and American white oaks finally were separated after 5.5mya. (Denk et.al. 2010) The red oaks were not successful in colonizing Europe, falling back to North America.

By start of the Pliocene (5.3mya), the last large changes to oak species diversification were occurring. (Hipp et.al. 2018) Interbreeding between the *Dumosae* group of what is today the far western white oaks and the *Prinoideae* (chestnut oaks) in today's eastern North America, occurrred. (Crowl et.al. 2019) The golden cup oaks *(Protobalanus)* were restricted to western North America during the Neogene (5 mya). (Denk et.al. 2017) By the beginning of the Pleistocene at 2.6 mya, and the beginning of the ice ages, the oak genus, groups, and species were considered genetically set and would have been recognizable today. (Hipp et.al. 2018)

Last Ice Age

In the last 15,000 to 18,000 years, North America saw its most recent ice sheet covering large parts of the Eastern United States. Figure 6 shows the ice sheet extent and extended coastal area due to a lowered sea level. All tree species were pushed South by the ice front to refuges in the Southern United States. Figure 7. Some species were pushed onto the exposed coastal flatwoods and some were driven into the sea. After glaciation, all of the oak species remaining began to migrate northward under improving climatic conditions. Figure 8. Oaks moved back up the Mississippi River Valley and along the western side of the Appalachians, filling valleys, mountainsides, and plains.

Climate Limitations On Oaks

Forest growth in the United States is controlled by lowest winter temperatures and average annual precipitation. Figure 9 shows the growth range (in temperature and precipitation) of all forest trees. Figure 10 overlays red oak species growth compared to all trees growing in the United States. Figure 11 shows white oak species growing across a range of temperatures and precipitation.

Today, most oak species grow in areas where the lowest Winter temperatures are between 14°F and 50°F, and the average annual precipitation is between 20-63 inches of rain. (Cavender-Bares et.al. 2018) Oaks have expanded across the continent and grew under a wide range of climates, except for very cold and very wet areas. (Cavender-Bares et.al. 2018) The eastern North American oaks showed a much broader precipitation range for growth than most other oaks, but are still excluded from very cold environments. (Cavender-Bares et.al. 2018)

Adaptive Advantage

Evergreen leaf forms of oaks are associated with more southern, warmer, and less variable / more stable temperatures requiems. (Hipp et.al. 2018) Live oaks (*Virentes* group) tend to grow well under warm temperatures and high precipitation conditions. Golden-cup oaks (*Protobalanus* group) tend to grow well under a dry, more Mediterranean climate. (Cavender-Bares et.al. 2018)

An ability to adapt and thrive under widely variable climatic conditions led to oak's successful colonization and distribution across North America over many millions of years. In eastern North America, the early arrival and rapid diversification of oak species during periods of expanding temperature zones generated great ecological success. (Cavender-Bares et.al. 2018) As environmental changes continued to occur, gene set selection pressure shifted, allowing unique and diverse adaptations, as well as stimulating species hybridization processes, which generated many useful variations and species. (Moran et.al. 2012)

Oak Species Groups

The broad genus group known as oaks today contain many species – some closely related and some distantly related – but all within the same genus (*Quercus*). Closely related species groups can, and have been found to, cross-breed or hybridize. More distantly related species within *Quercus* seldom, if ever, hybridize. The genetic relatedness or closeness of different oak species to each other, and their ability to naturally hybridize, has lead them to be categorized into separate species groups.

Groupings for North American oaks were first developed in 1924 as *Leucobalanus* (white oaks), *Erythrobalanus* (red oak), and *Protobalanus* (golden cup oaks). (Denk et.al. 2017) These group names were used for decades in botanical, horticultural, and forestry literature. Species in these oak groups can grow beside each other and not hybridize between the groups, with each species group maintaining its unique morphological signature.

A New Ordering

In the last ten years, *Quercus* genus groups have been more formalized and used in descriptions of different oak species. The genus *Quercus* has been divided into two sub-genera: Subgenus *Cerris*, the eurasian, old world, mid-latitude, or palearctic-indomalayan oak group; and, Subgenus *Quercus*, the new world, high latitude, or nearctic oak group. Figure 12 (Denk et.al. 2010; Denk et.al. 2017; Hubert et.al. 2014) Each sub-genus is divided into a number of sub-groups or sections. Figure 13 shows the proportion of each sub-division among all *Quercus* species.

Sub-genus *Cerris* is divided into three sections, all from eurasia, East Asia, and North Africa. The first section is by far the largest of the three, Section *Cyclobalanus,* the East Asian cycle-cup oaks with ~101 species (i.e. *Quercus myrsinifolia*). The second section is Section *Cerris*, the eurasian and North African cerris oaks with ~13 species (i.e. *Quercus acutissima*). The final section is Section *Ilex,* the eurasian and North African holly oaks (*Heterobalanus* group) with ~35 species (i.e. *Quercus ilex*) (Denk et.al. 2010; Denk et.al. 2017; Hubert et.al. 2014) Another historic sub-division of old world oaks was section *Sclerophyllodrys* which was represented by three evergreen, sclerophyllous euro-mediterranean oaks, but is now not accepted as a standard division. (Hubert et.al. 2014) Figure 14.

Quercus -- *Quercus*

The second Sub-genus *Quercus* is divided into a number of sections which vary by author. Section *Quercus* is the North America and eurasian white oaks (*Leucobalanus* group) with ~160 species (i.e. *Quercus alba*). Section *Ponticae* is comprised of two disjunct species, one from Western eurasian and one from Western North America (i.e. *Quercus pontica*). Section *Virentes* is the North American southern live oaks with ~7 species (i.e. *Quercus virginiana*). Section *Lobatae* is the North American red oaks (*Erythrobalanus* group) with ~162 species (*i.e. Quercus nigra*). Section *Protobalanus* is the southwestern United States and northwestern Mexico golden-cup oaks with ~5 species (i.e. *Quercus chrysolepis*). (Denk et.al. 2010; Denk et.al. 2017; Hipp et.al. 2014; Hubert et.al. 2014; McVay et.al. 2017a; Pham et.al. 2017) Figure 15.

The Sub-genus *Quercus*, Section *Quercus* is further subdivided into closely related white oak groups. In order of their relatedness to each other, the sub-sections are: *Dumosae* – California white oaks (*Quercus douglasii*); *Prinoideae* – chestnut oaks (*Quercus prinoides*); *Albae* – white oaks (*Quercus alba*); *Roburoids* – eurasian white oaks (*Quercus robur*); *Stellatae* – post oaks (*Quercus stellata*); and, *Leucomexicanae* – Mexican white oaks (*Quercus polymorpha*). Figure 16. (Crowl et.al. 2019; McVay et.al. 2017a; Pham et.al. 2017) For example, the least related of the new world white oaks are the *Dumosae* and the *Leucomexicanae*, and the two more closely related sub-sections are the *Prinoideae* and *Albae*. (Crowl et.al. 2019; Denk et.al. 2010; Denk et.al. 2017; Hipp et.al. 2014; Hubert et.al. 2014; McVay et.al. 2017a; Pham et.al. 2017)

Quercus -- Red

The Sub-genus *Quercus*, Section *Lobatae* (red & black oaks) is further subdivided into closely related oak groups. In order of their relatedness to each other, the sub-sections are: *Pagodaefoliae* – southern red oaks (*Quercus falcata*); *Ilicifoliae* – bear oaks (*Quercus ilicifolia*); *Laurifoliae* – laurel oaks (*Quercus laurifolia*); *Velutinae* – black oaks (*Quercus velutina*); *Palustres* – pin oaks (*Quercus palustris*); *Coccineae* – red oaks (*Quercus rubra*); *Marilandicae* -- blackjack oaks (*Quercus marilandica*); *Nigrae* -- water oaks (*Quercus nigra*); *Erythromexicanae* -- Mexican red oaks; and, *Agrifoliae* -- far Western red oaks (*Quercus agrifolia*). Figure 17. For example, the least related of the new world red oaks are the *Pagodaefoliae* and the *Agrifoliae*, and the two more closely related sub-sections are the *Coccineae* and *Palustres*. (Hauser et.al. 2017; Moran et.al. 2012; Solomon 1983; Sullivan et.al. 2016)

Summarizing

Figure 18 provides a summarry of the *Quercus* genus, *Quercus* sub-genus, *Quercus* and *Lobatae* sections (white and red oaks), and associated sub-sections of white and red oaks. Over a number of

years and authors, sub-sections of white and red oaks have varied greatly with some groups split off and some groups consolidated.

Distribution of oaks in North America, divided by regions are: Eastern United States = 36 oak species (18 red, 16 white, 2 live) – of these 33 are in the southeastern United States; Western United States = 29 oak species (15 white, 13 red, 1 live); Far Western United States = 9 oak species (3 red, 4 white, 1 golden cup); and, Mexican = 145 oak species. (Cavender-Bares et.al. 2018) Figure 19

Questions About Live Oaks

Live oak is the State Tree of Georgia, and is of great historic and ecological value as a native tree. Live oaks are in the Sub-genus *Quercus* – Section *Virentes* with seven species. Live oaks are in the white oak group. The live oak section is split into: southern live oak (*Quercus virginiana*), sand live oak *(Quercus geminata*), and dwarf live oak (*Quercus minima*) within an Eastern live oak group (all native to Georgia); Cuban oak (*Quercus sagraeana*) and encino (*Quercus oleoides*) within a southern live oak group; and, the rare Brandegee oak (*Quercus brandegeei*) and Texas live oak (*Quercus fusiformis*) within a western live oak group. (Eaton et.al. 2015)

One of these live oak species is the Cuban oak (*Quercus sagraeana*). There has been great debate regarding how the Cuban oak developed. One research group has stated during the Pleistocene (~0.5 mya), southern live oak (*Quercus virginiana)* had limited migration from Florida to Cuba. Once in Cuba, the isolated live oak population generated the Cuban oak. The Cuban oak shows no evidence of a hybrid origin, but became a species due to isolation of a small population with limited genetic source material. (Gugger & Cavender-Bares 2013)

At a later time, with limited dispersal and hybridization of Cuban oak (*Quercus sagraeana*), encino *(Quercus oleoides)* in Central America (i.e. Belize & Honduras) developed. (Gugger & Cavender-Bares 2013) It was found Cuban oak (*Quercus sagraeana*) is most closely related to southern live oak (*Quercus virginiana)*, and most distantly related to sand live oak *(Quercus geminata)*. The genetic relationship with encino (*Quercus oleoides)* is intermediate. (Gugger & Cavender-Bares 2013) Alternatively, another research group has determined Cuban oak was derived from a Central American origin. (Eaton et.al. 2015)

Conclusions

Oak is the largest and most dominant tree genus of North America and the Northern Hemisphere. Oaks are widely distributed across many habitats, and growing under many conditions. The three North America oak groups (white, red / black, and golden-cup) represent roughly 60% (~255) of the ~435 species within the *Quercus* genus worldwide. Georgia's native oak species, and their natural hybrids, represent a great ecological asset to the State.

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Genus = *Quercus* / oak

A. Sub-genus = *Quercus*

Sections:

A1. *Quercus* – white oaks (*Lepidobalanus* or *Leucobalanus*)
A2. *Virentes* -- live oaks
A3. *Ponticae* (*Mesobalanus*)
A4. *Protobalanus* -- golden-cup oaks
A5. *Lobatae* (*Erythrobalanus*) -- red oaks

B. Sub-genus = *Cerris*

Sections:

B1. *Cyclobalanopsis* -- cycle-cup oaks
B2. *Cerris* -- cerris oaks
B3. *Ilex* (*Heterobalanus*) -- holly oaks

Figure 1: Genus, sub-genus, and sections of oak.

Cenophytic Era --

Age of Angiosperms -- Flowering Plants

Quaternary	**0 - 2.6mya**
Holocene	0 - 0.01mya
Pleistocene	0.01 - 2.6mya
Neogene	**2.6 - 23mya**
Pliocene	2.6 - 5.3mya
Miocene	5.3 - 23mya
Paleogene	**23 - 66mya**
Oligocene	23 - 34mya
Eocene	34 - 56mya
Paleocene	56 - 66mya

Mesophytic Era --

Age of Gymnosperms -- Seed Plants

Cretaceous	**66 - 145mya**
Jurassic	**145 - 206mya**
Triassic	**206 - 248mya**

Figure 2: Geologic time periods listed in millions of years ago (mya) values.

Order= *Fagales*

Family= *Fagaceae*

(~10 genera ~927 species)

A. Sub-Family = *Fagoideae*

1. ***Fagus*** = beech (~12 sp. – e-sw Asia, Europe, & e North America)

B. Sub-Family = Castaneoideae

2. ***Castanea*** = chestnut (10 sp. – e-sw Asia, se Europe, & e North America)
3. ***Castanopsis*** = chinkapins (~120 sp. – se Asia)
4. ***Chrysolepis*** = *golden chinkapin (2 sp. – w US)*

B. Sub-Family = *Quercoideae*

5. ***Trigonobalanoids*** = *(3 genera – 1 species each -- se Asia & Columbia)*
6. ***Lithocarpus*** = *stone oak (~300 sp. – Asia)*
7. ***Notholithocarpus*** = *tanoak (1 sp. – w US)*
8. ***Quercus*** = *oak (~500 sp. – Northern Hemisphere & Indonesia)*

NOTE: old genus *Nothofagus* -- southern beech (~35 species -- Southern Hemisphere) -- now separate family *Nothofagaceae*.

Figure 3: Order, family, and sub-family of oak species.
(after Manos et.al. 2001)

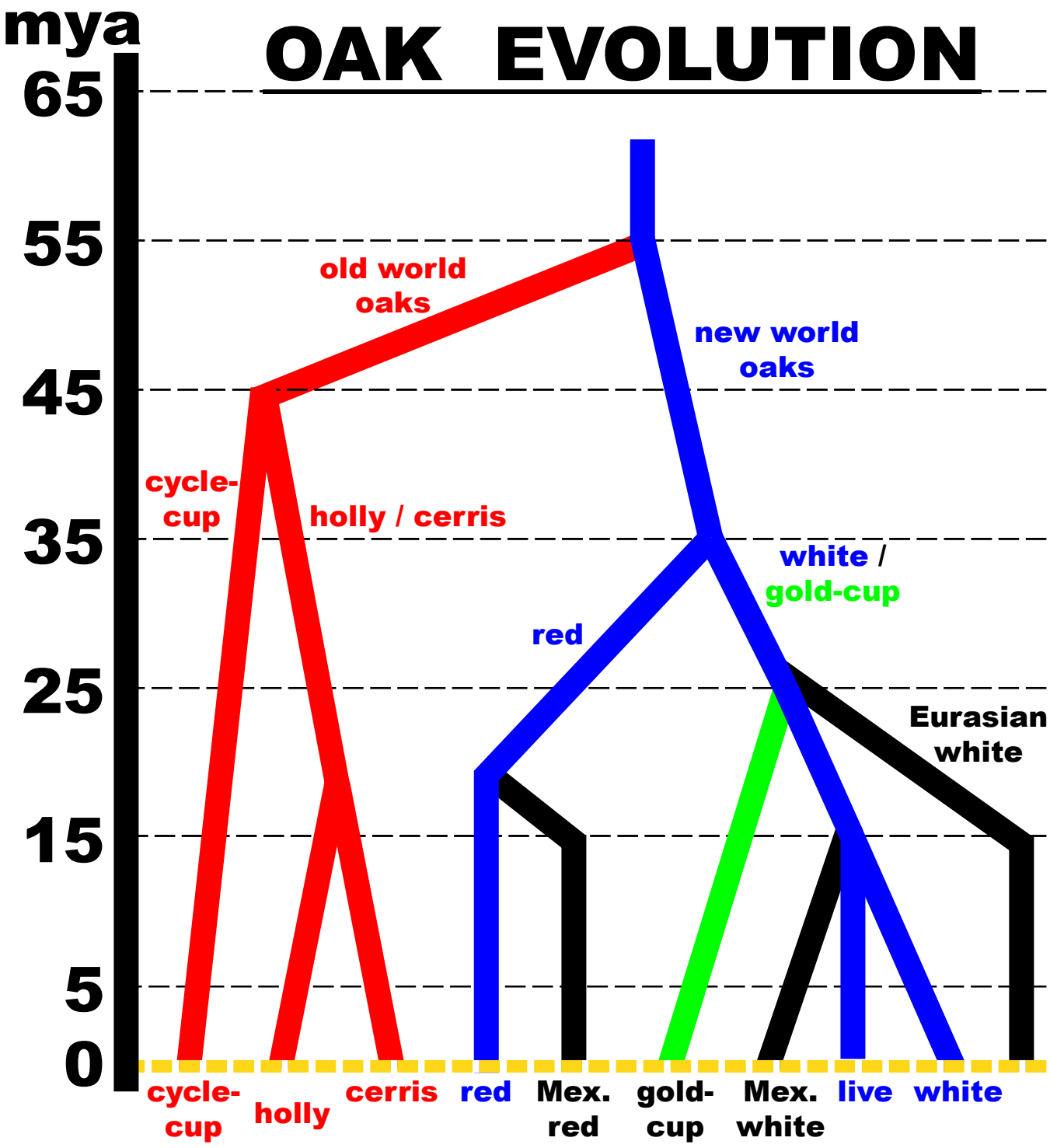

Figure 4: Time-line of oak species groups evolution, diversification, and divergence in millions of years before present (i.e. mya). Blue lines lead to native oak species.
(see text for various author citations and oak name descriptions)

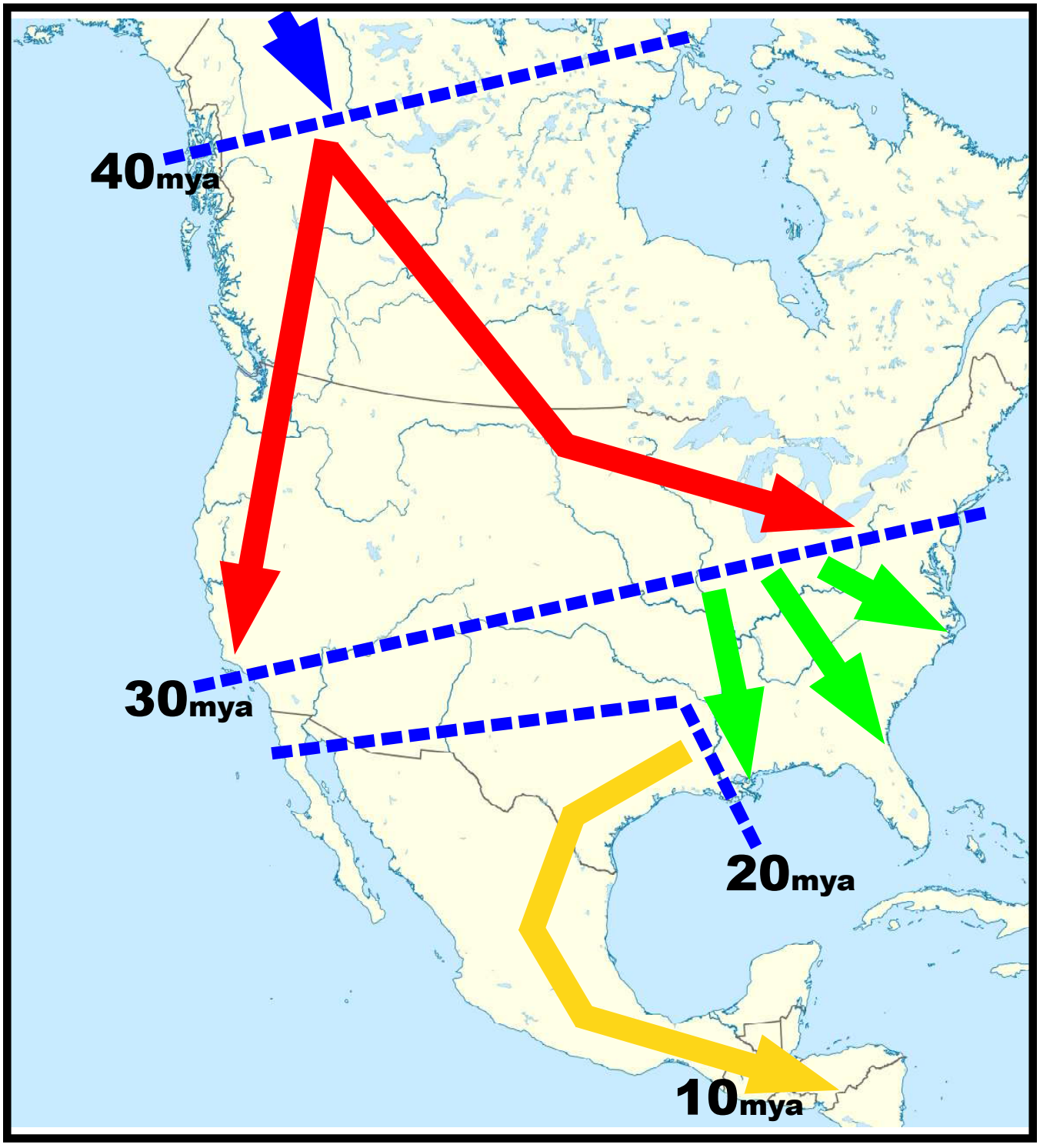

Figure 5: Expansion and diversifying of *Quercus* (oak) genera across North America over 40 million years.
(Cavender-Bares et.al. 2018)

Figure 6: Extent of last glaciation ice sheets and exposed coast line ~18,000 years ago.

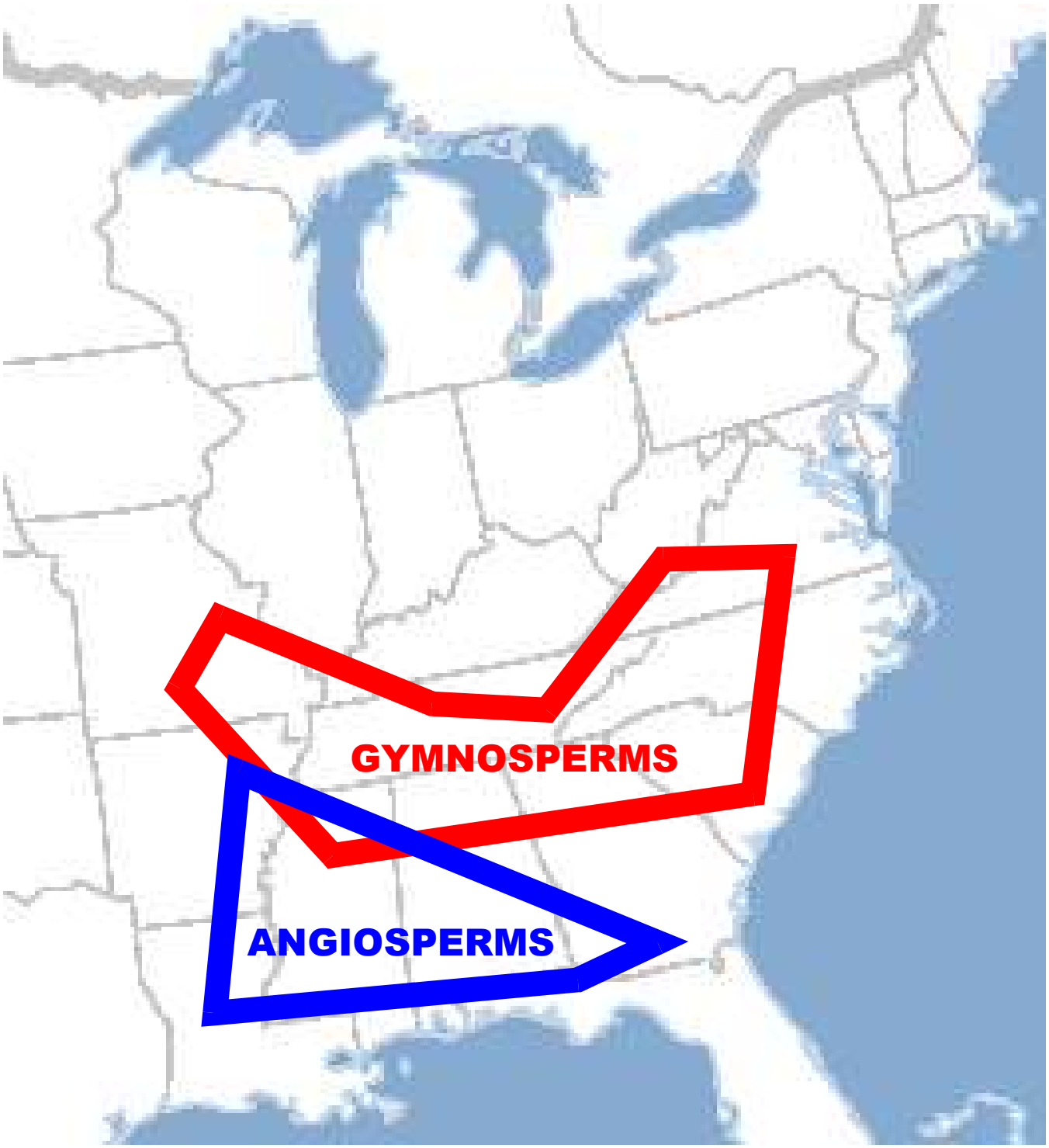

Figure 7: Last glacial refuge areas for *Gymnosperms* and *Angiosperms* (i.e oaks) in eastern North America.
(Davis 1981)

Figure 8: Glacial refuge area in Southern US for *Quercus* species, and direction of migration after glaciation.
(Davis 1981)

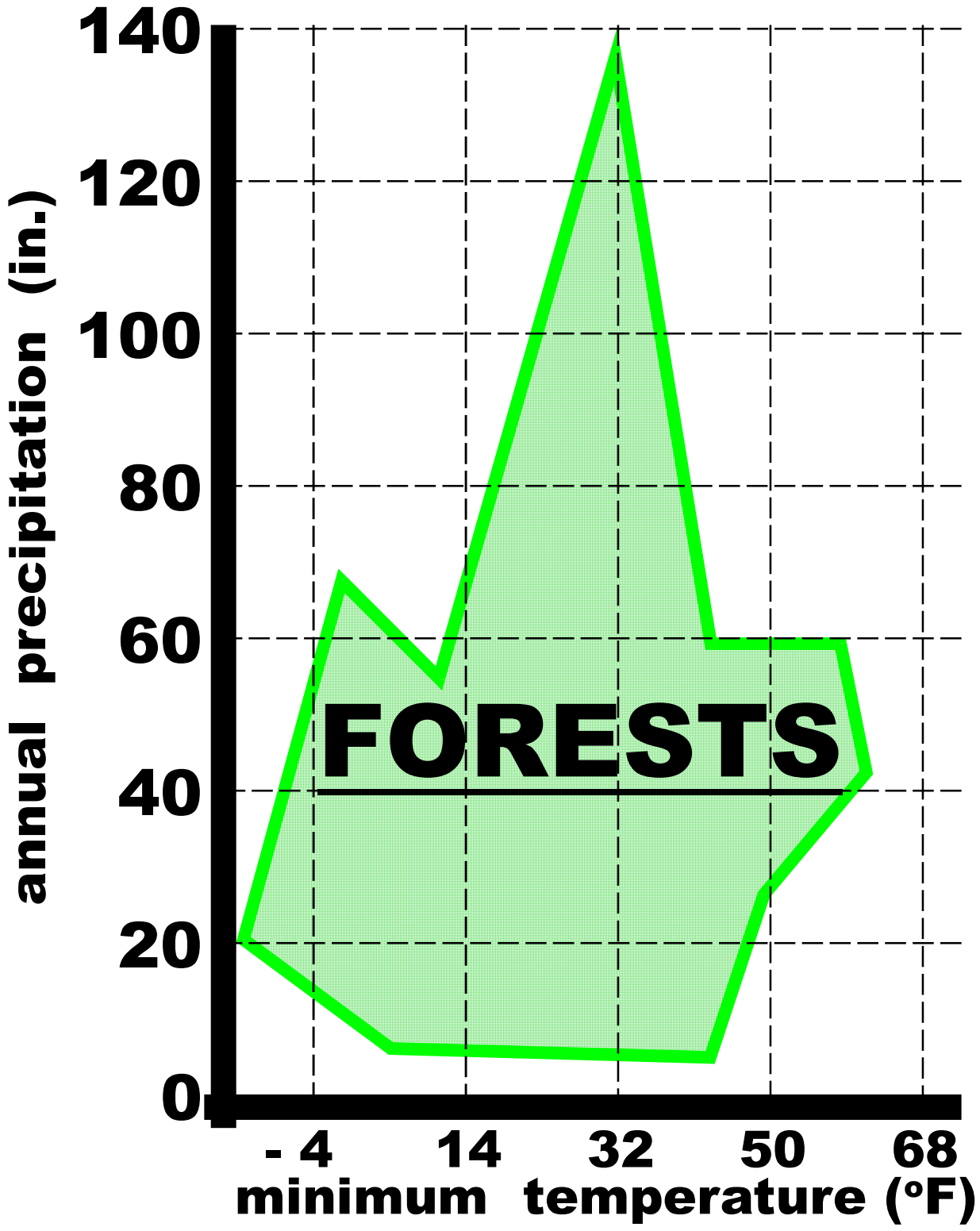

Figure 9: Continental United States forest climatic distribution using minimum temperature in the coldest month and average annual precipitation. (derived from Cavender-Bares et.al. 2018)

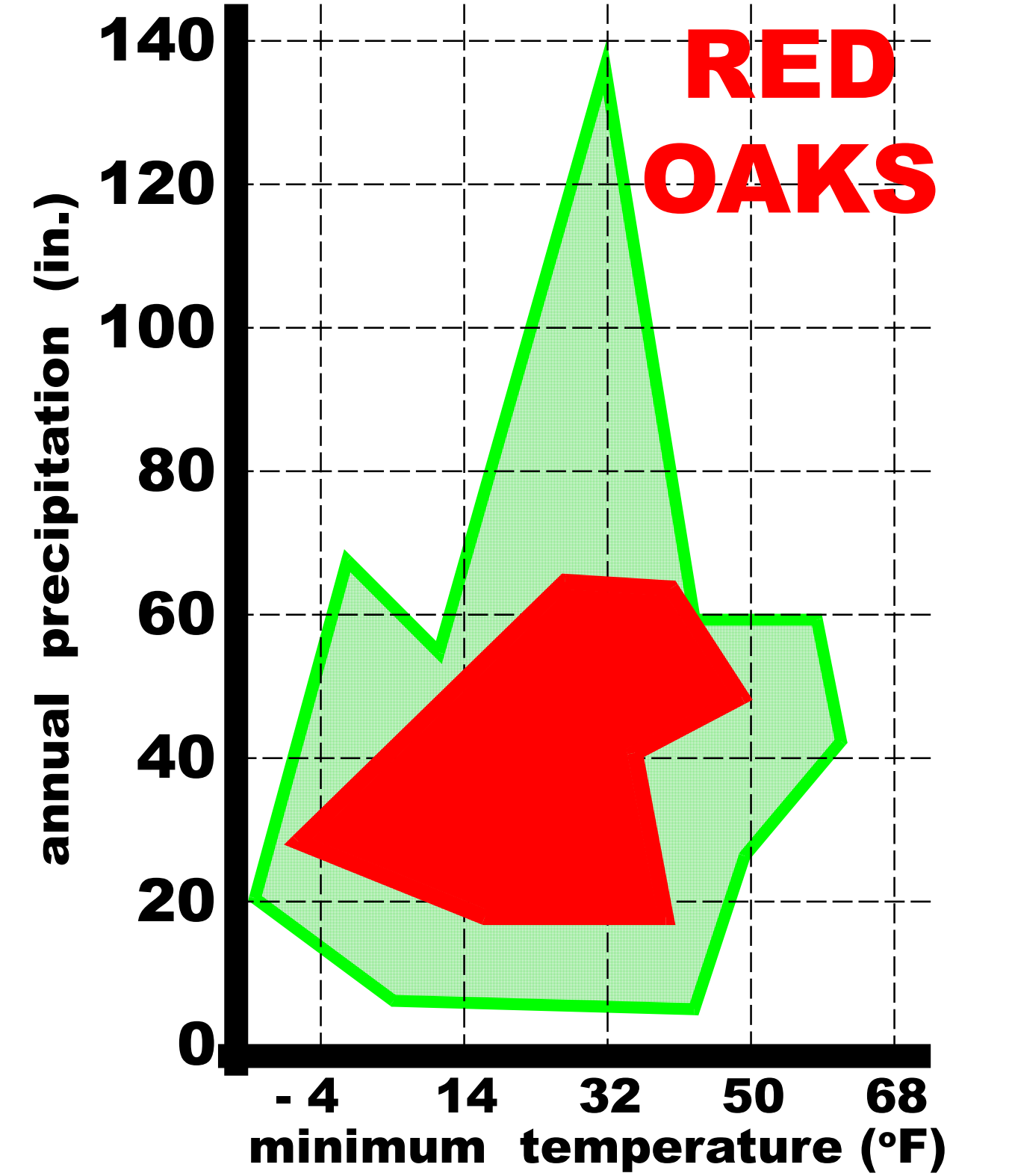

Figure 10: Continental United States climatic distribution of red oak group. (derived from Cavender-Bares et.al. 2018)

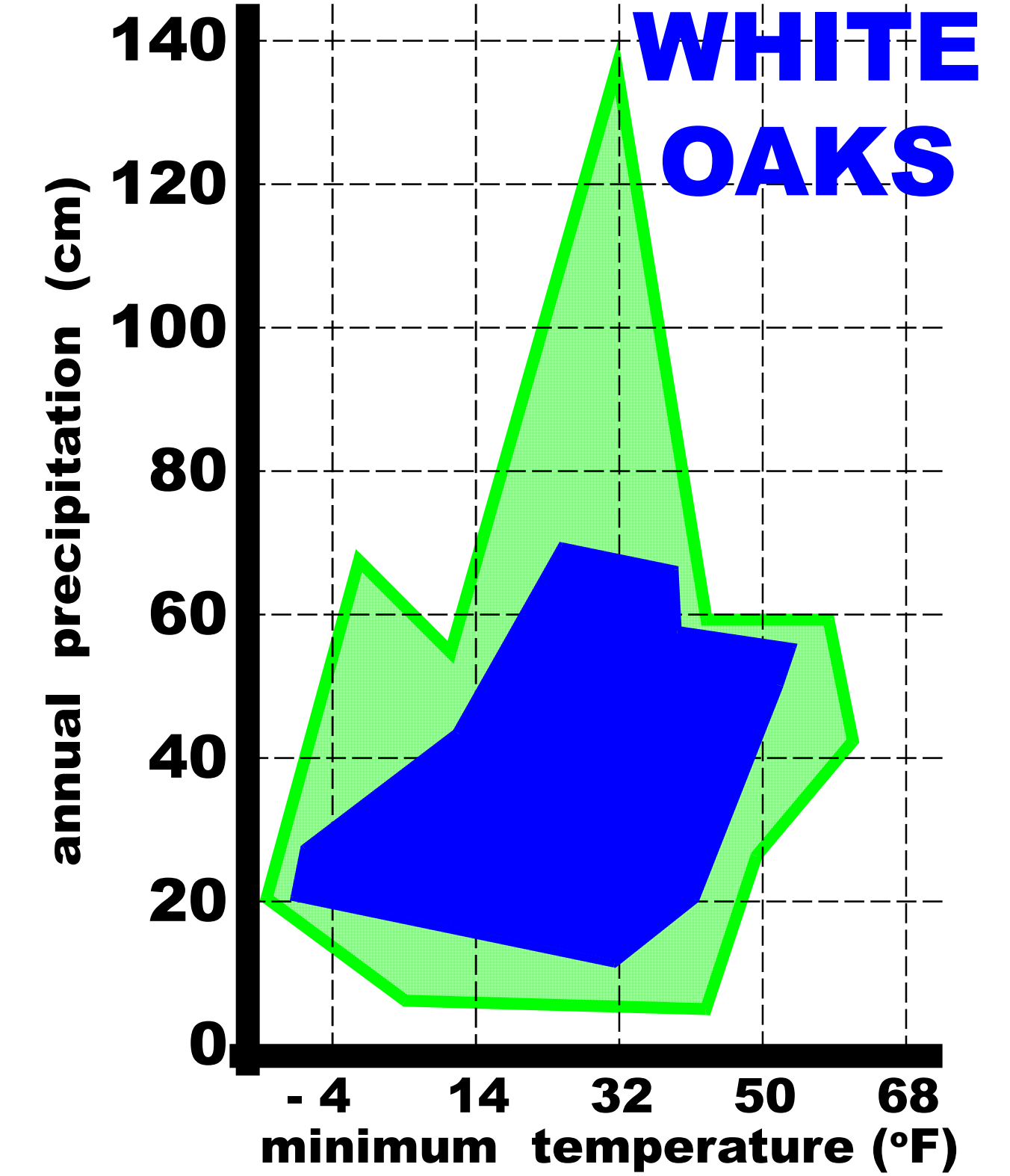

Figure 11: Continental United States forest climatic distribution of white oak, live oak, and golden-cupoak groups.
(derived from Cavender-Bares et.al. 2018)

Subgenus *Cerris*

(Eurasian Old World group – mid-latitude clade)

Section *Cyclobalanus*

(cycle-cup oaks) ~101 species

(Quercus myrsinifolia)

Section *Cerris*

(cerris oaks) ~13 species *(Quercus acutissima)*

Section *Ilex*

(holly oaks) ~35 species *(Quercus ilex)*

Subgenus *Quercus*

(New World group – high latitude clade)

Section *Quercus*

(white oaks) ~160 species *(Quercus alba)*

Section *Ponticae*

(disjunct species group) ~2 species

(Quercus pontica)

Section *Virentes*

(live oaks) ~7 species *(Quercus virginiana)*

Section *Lobatae*

(red oaks) ~162 species *(Quercus nigra)*

Section *Protobalanus*

(golden-cup oaks) ~5 species

(Quercus chrysolepis)

Figure 12: List of *Quercus* (oak) subgenera and sections.
(Crowl et.al. 2019; Denk et.al. 2010; Denk et.al. 2017; Hipp et.al. 2014; Hubert et.al. 2014; McVay et.al. 2017a; Pham et.al. 2017)

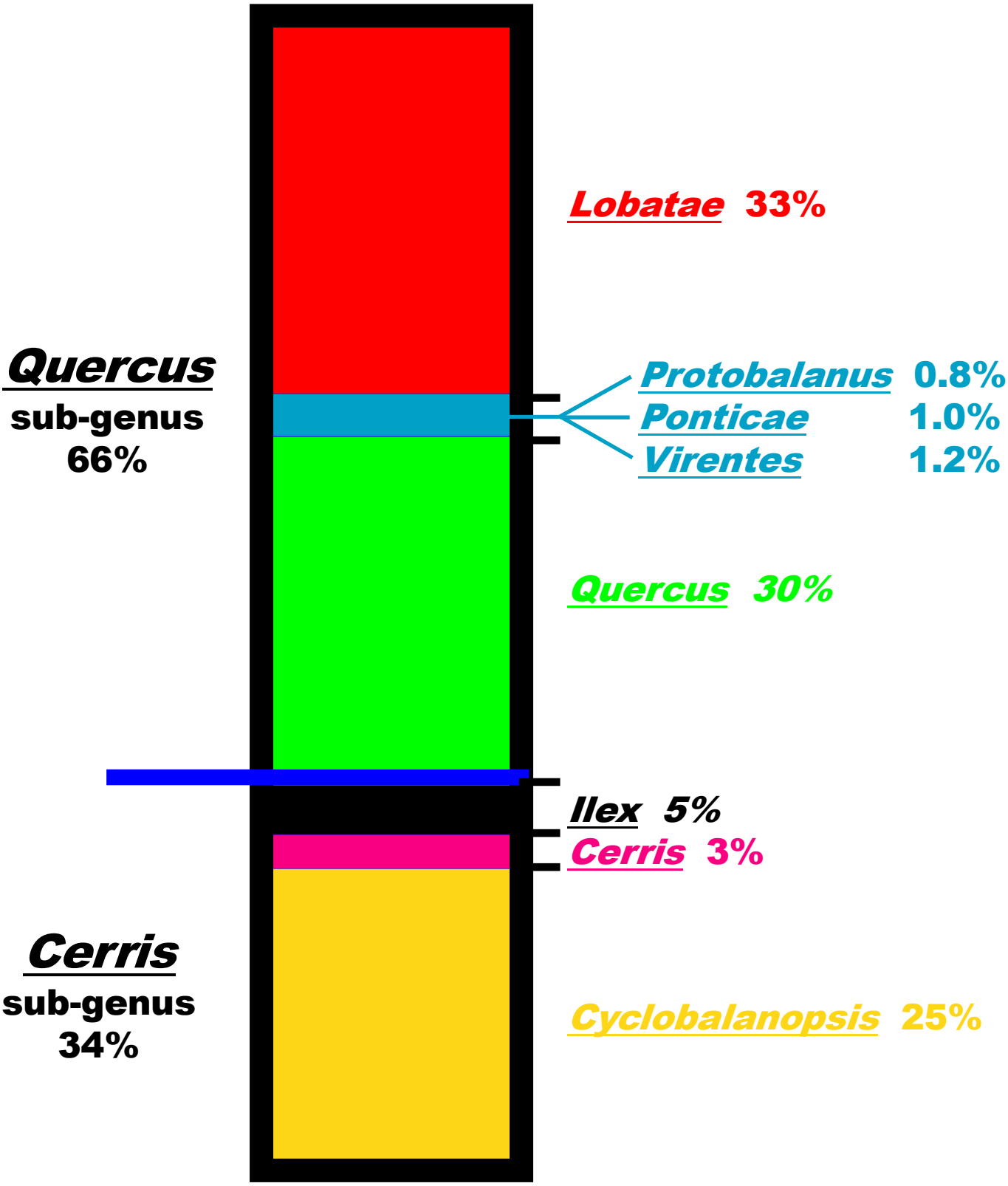

Figure 13: Proportions of species within sub-genus and section groups in *Quercus* (oak).

Genus = *Quercus* (oak)
Sub-Genus = *Cerris*

tropical & sub-tropical oaks of Asia / Eurasia / N. Africa

Sections:

Cyclobalanopsis **-- Asian cycle-cupped oaks**

-- e-se Asia --
~150 species / 25% of total
Q. acuta **- Japanese evergreen oak**
Q. glauca **- Japanese blue oak**

Cerris **-- cerris oaks**

-- Eurasian / n Africa --
~18 species / 3% of total
Q. cerris **- Turkey oak**
Q. ithaburensis **- Mount Tabor oak**
Q. acutissima **- sawtooth oak**

Ilex **-- holly oaks**

-- Eurasian & n Africa --
~32 species / 5% of total
Q. ilex **- holly oak**
Q. coccifera **- kermes oak**
Q. calliprinos **- Palestine oak**

(~200 species in *Cerris* sub-genus -- 34% of total)

Figure 14: Sub-genus *Cerris* sections and example species. Number of species in each section varies by author.

Genus = *Quercus* (oak)

(~592 species – 4,529 named & synonyms)

Sub-genus = *Quercus*

Sections:

Quercus (***Lepidobalanus*** or ***Leucobalanus***) -- white oaks

~180 species / 30% of total -- (*Q. alba* - white oak)
w Eurasia, e Asia, North America, Central America, n Africa

Virentes -- live oaks -- NA, Carribean, Central America

7 species / 1% of total -- (*Q. virginiana* - live oak)

Ponticae (***Mesobalanus***) white oaks – Eurasia, w NA

~2-6 species / 1% of total -- Armenian oak, deer oak
(*Q. pontica*; *Q. sadleriana*)

Protobalanus golden-cup oaks -- sw United States, nw Mexico

~5 species / <1% of total
(*Q. chrysolepis* - canyon live oak)

Lobatae (***Erythrobalanus***) red oaks -- NA, California, Columbia

~195 species / 33% of total
(*Q. rubra* - northern red oak)

(~393 species in *Quercus* sub-genus -- 66% of total)

Figure 15: Sub-genus *Quercus* sections in order of relatedness. Number of species in each section varies by author.

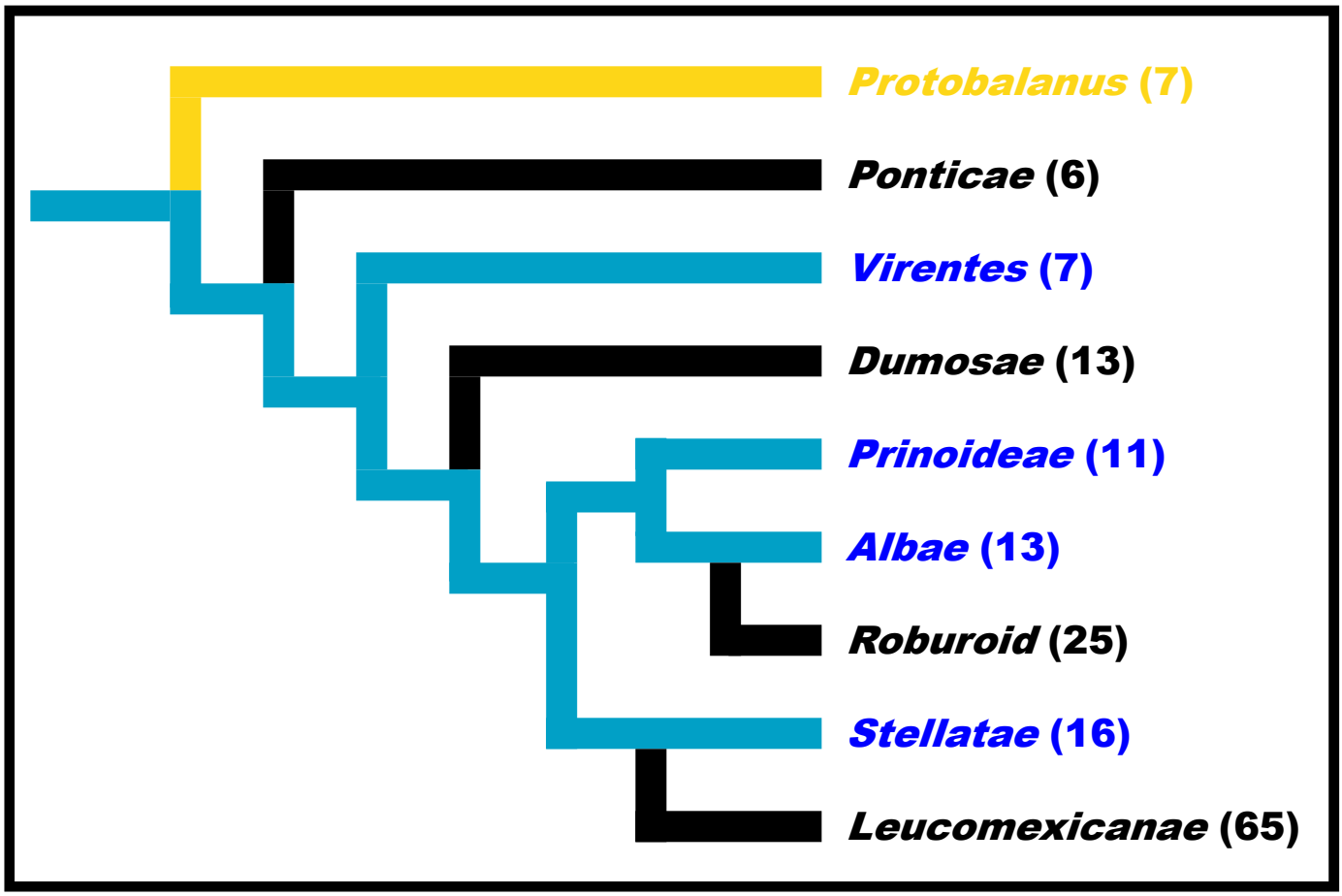

Figure 16: Relationship between white oak groups and golden-cup oak group. Light blue (cyan) lines represent groups containing native Georgia oak species. Numbers are member species and their inclusion varies by author.
(derived from McVay et.al. 2017a)

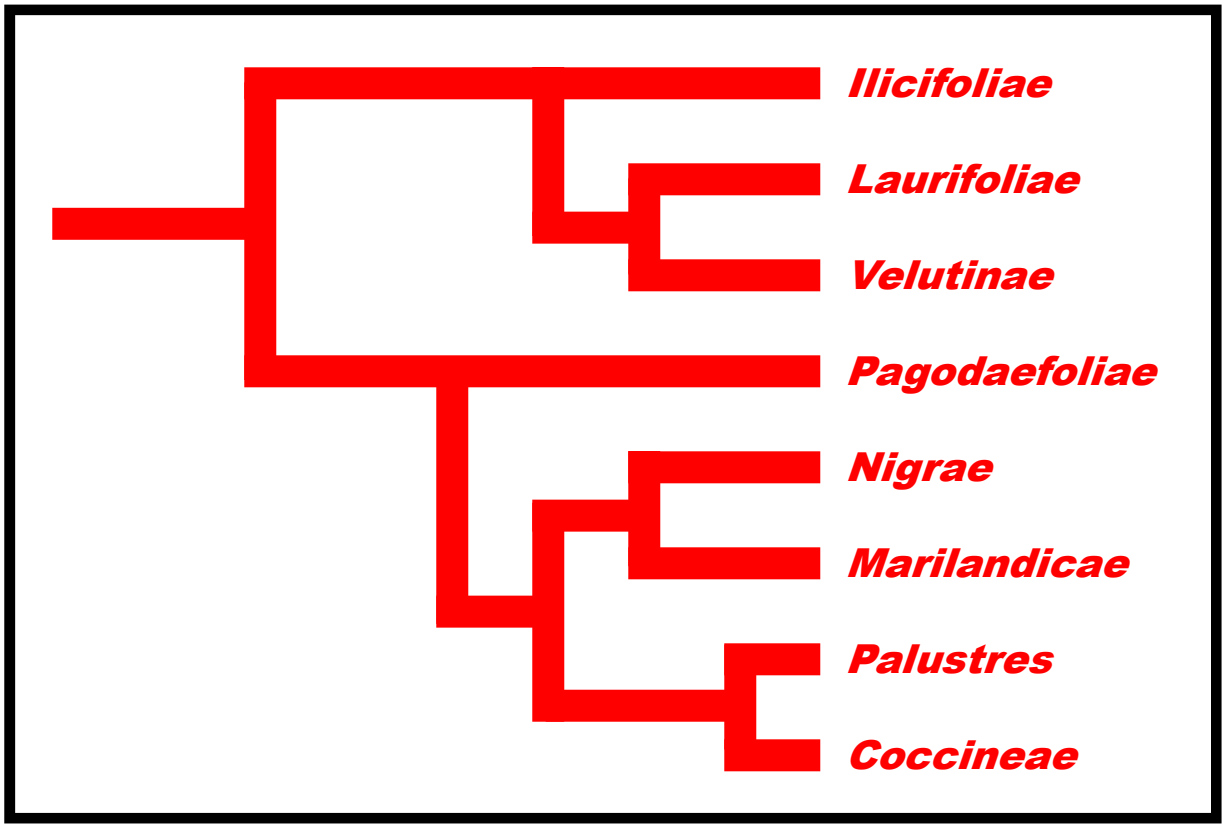

Figure 17: Relationship between red oak groups (*Lobatae*) of native Georgia oak species.
(derived from Solomon 1983)

Quercus Genus, *Quercus* Sub-Genus

2 Sections & Sub-Sections:

Quercus (*Lepidobalanus* or *Leucobalanus*)

white oaks

~180 species / 30% of total in genus --
w Eurasia, e Asia, North America, Central America, n Africa

sub-sections:

Roburoids	**~25 species**	(***Q. robur*** **- Eurasian white oak)**
Lobatoids	**~ 9 species**	(***Q. lobata*** **- valley oak)**
Dumosae	**~ 6 species**	(***Q. dumosa*** **- CA scrub oak)**
Prinoideae	**~11 species**	(***Q. prinoides*** **- dwarf chestnut oak)**
Albae	**~13 species**	(***Q. alba*** **- white oak)**
Stellatae	**~16 species**	(***Q. stellata*** **- post oak)**
Polymorphae	**~ 5 species**	(***Q. polymorpha*** **- Mexican white oak)**
Leucomexicanae	**~100 species**	**(s-sw-NA white oaks)**

Lobatae (*Erythrobalanus*)

red oaks

~195 species / 33% of total in genus --
North America, Central America, Columbia

sub-sections:

Pagodaefoliae		(***Q. falcata*** **- southern red oak)**
Ilicifoliae		(***Q. ilicifolia*** **- bear oak)**
Laurifoliae	**~15 species**	(***Q. laurifolia*** **- swamp laurel oak)**
Velutinae		(***Q. velutina*** **- black oak)**
Palustres	**~2 species**	(***Q. palustris*** **- pin oak)**
Coccineae	**~8 species**	(***Q. rubra*** **- northern red oak)**
Marilandicae		(***Q. marilandica*** **- blackjack oak)**
Nigrae		(***Q. nigra*** **- water oak)**
Erythromexicanae	**~90 species**	(***Q. mexicana*** **- s-NA red oaks)**
Agrifoliae	**~4 species**	(***Q. agrifolia*** **- California live oak)**

Figure 18: Two sub-genus *Quercus* sections and subsections in order of relatedness. Number of species in each sub-division varies by author.

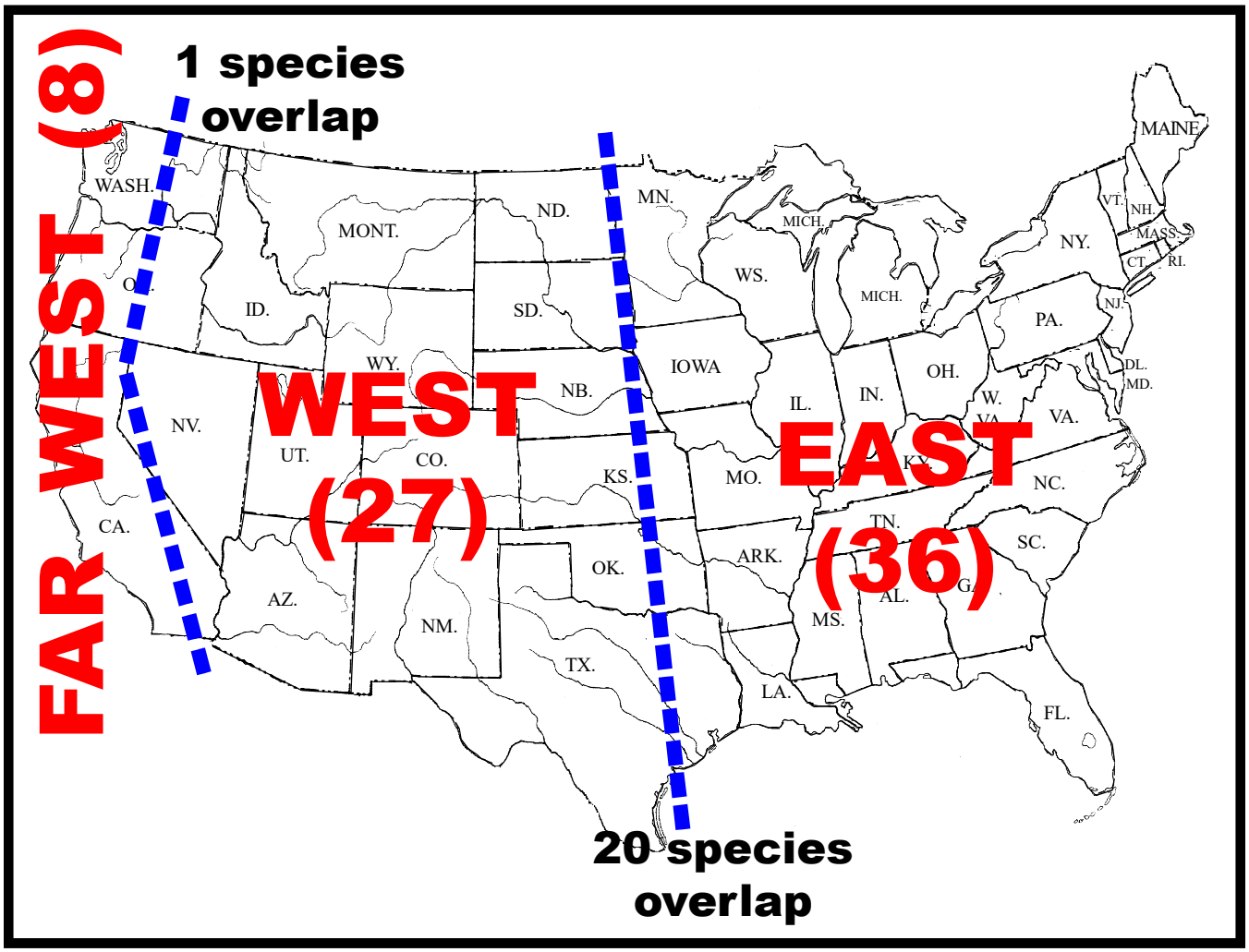

Figure 19: Regional distribution of forty-nine surveyed *Quercus* (oak) species across the United States.
(Cavender-Bares et.al. 2018)