1 Global and Neotropical Distribution and Diversity of Oak (genus *Quercus*) and Oak Forests

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1.1 Introduction

The genus *Quercus* is one of the most important clades of woody angiosperms in the northern hemisphere in terms of species diversity, ecological dominance, and economic value. Oaks are dominant members of a wide variety of habitats, including temperate deciduous forest, temperate and subtropical evergreen forest, subtropical and tropical savannah, subtropical woodland, oak-pine forest, oak-'piñon'-juniper woodlands, various kinds of 'cloud forest', tropical premontane forest, tropical montane forest, matorral (summer rain chaparral), and a variety of Mediterranean climate vegetations, including chaparral (French: maqui), oak woodland, and evergreen oak forest (Nixon 1993a, b, 1997b, 2002; Kappelle et al. 1995). Oaks also enter, and are important, along the margins of various other vegetation types, such as coniferous forests, prairies, tropical grasslands, desert and semi-desert scrublands, dry (deciduous) tropical forest, and in some evergreen tropical forests (Barbour and Billings 1999).

Although many species of *Quercus* are exceptionally large, dominant overstory trees (Kappelle et al. 1995, Chaps. 8–11 and 14–17), perhaps an almost equal number of species are shrubs or small trees, particularly in drier habitats such as chaparral, in edaphically challenging environments, and in some higher elevation forests. Oaks also occur as 'specialists' in a diversity of edaphically distinct habitats, such as serpentine, sandy barrens, and swamps. However, in wetter forests oaks are often among the largest trees of the region, particularly when compared to other angiosperms. In the Americas, this is true both in the temperate deciduous forests of the eastern USA and in the evergreen oak forests of Mexico and Central America. Oaks also occur in the Himalayas and Southeast Asia (Indonesia).

The economic importance of *Quercus* in the northern hemisphere is widely known. Various species are sources of high-quality lumber, and it is the

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preferred firewood in many areas, particularly as a cooking/heating fuel throughout the highlands of Mexico and Central America. Because of the dominance of oak in many forests, it is the subject of a vast number of ecological studies that focus on interactions between oaks and fungi (Chap. 5), plants (Chaps. 18, 19 and 23) and animals (Chaps. 24–27).

1.2 Higher-Level Taxonomy

The genus *Quercus* in the broad sense is a member of the family Fagaceae (excluding *Nothofagus*), which also includes *Fagus* (beeches), *Castanea* (the true chestnuts), other 'castaneoid' genera (*Chysolepis*, *Castanopsis*, and *Lithocarpus*), and three monotypic tropical genera (*Trigonobalanus*, *Formanodendron*, and *Colombobalanus*). In the New World, in addition to *Quercus* we have *Fagus* (two spp.), *Chrysolepis* (one spp.), *Lithocarpus* (one sp.). *Castanea* (two spp.), and *Colombobalanus* (one spp.; Nixon and Crepet 1989; Nixon 1997a, 2003). The family Fagaceae sensu stricto (excluding *Nothofagus*) is monophyletic, based on both morphological and molecular analyses (Nixon 1989; Manos et al. 1999). In the recent literature, oaks are treated either as a single genus with two subgenera (*Quercus* and *Cyclobalanopsis*; Nixon 1993b), or as two distinct genera (*Quercus* and *Cyclobalanopsis*). The evidence at this point, based on molecular data, is equivocal as to whether *Quercus* and *Cyclobalanopsis* form a monophyletic group (P.S. Manos, personal communication). In the Flora of China, the two lineages were separated as distinct genera, with 35 species recognized for *Quercus*, and 69 species of *Cyclobalanopsis* within China (Chengyiu et al. 1999). Within the New World, only *Quercus* sensu stricto occurs (Nixon 1997b; Nixon and Muller 1997), so the issue of whether to recognize one or two genera (thankfully) does not affect the nomenclature in this region.

Within New World *Quercus*, there have been traditionally recognized three distinct groups – the white oaks (section *Quercus*, sometimes referred to as subgenus or section *Leucobalanus* or *Lepidobalanus*), the red or black oaks (section *Lobatae*; also sometimes referred to as subgenus or section *Erythrobalanus*), and the intermediate or golden oaks (section *Protobalanus*; Nixon 1993a, b, 1997b; Manos 1997). A fourth group, section *Cerris*, is restricted to Eurasia and North Africa. Sections *Quercus* and *Lobatae* are widespread in the Americas and relatively diverse, whereas section *Protobalanus* is a small clade of ca. six species restricted to the southwestern USA and northern Mexico, including some islands near the west coasts of both countries (the Channel Islands, Guadalupe Island, and Cedros Island; see Manos 1997). Section *Quercus* is widespread in the northern hemisphere of the Old World in addition to the Americas, whereas section *Lobatae* and *Protobalanus* are both endemic to the New World.

The genus *Quercus* first appears in the fossil record in the Early Tertiary of North America about 50–55 million years ago (Crepet and Nixon 1989a, b), although the oldest evidence for the family Fagaceae is in the Late Cretaceous, about 90 million years ago (Crepet et al. 2004). Although in both cases the earliest records are North American, this is likely due to sampling error, and the biogeographic origins of both *Quercus* and Fagaceae remain equivocal at this point (Nixon 1989). By the mid to late Tertiary, *Quercus* fossils are among the most common found at numerous localities in western North America, suggesting that widespread (evergreen) oak forests occurred over wide areas in the northern hemisphere, particularly in the Miocene. In Chapter 2, Hooghiemstra provides information (from fossil pollen records) on the immigration of *Quercus* in the Colombian Andes.

From the perspective of oak taxonomy and systematics, several aspects of the genus are important. For one, the oaks are considered exceptional for their apparent ability to hybridize within species groups. This is based mostly on observations that species are highly variable, often with isolated individuals and occasionally with significant populations showing morphological variability that encompasses characteristics of more than one recognized species. Numerous studies have attempted to document and characterize hybridization among oak species, and in the last part of the 20th Century, several studies employed genetic and/or molecular markers to address questions of hybridization. In addition to documenting obvious cases of morphological introgression, some studies also found that cryptic hybridization could be present, as evidenced by the distribution of plastid types that seemed to be independent of species boundaries, but correlated instead with geographic proximity of populations. For example, within European white oaks, it was found that *Quercus robur* and *Q. petraea* populations in close proximity shared the same chloroplast genome, whereas they differed from conspecific populations from more distant localities. This was also found in at least one US study (Whittemore and Schaal 1991).

More recently, based on similar kinds of observations, it has been suggested that *Quercus* species may accomplish at least some dispersal solely through pollen transport by wind; pollen reaching relative populations of a related species might produce hybrids, and eventually through repeated backcrossing and selection, the 'invading' species emerges and produces its own morphologically distinct populations, similar to those that produced the pollen. Such scenarios might explain the pattern of morphological variation that is seen throughout the range of *Quercus*, and in some specific cases, putative hybrids (morphological intermediates) are well-known outside the geographic or ecologic range of one of the parents (Nixon 1993b). Whether these cases are due to past contact of populations followed by swamping of one of the parents, or rather to pollen dispersal over long distances remains to be seen. It is important to note that natural hybrids have been documented only between species within the same section. Although there have been scattered reports of artificial hybridization between species from different sections, these have not been verified with genetic or molecular data.

When considering the nature of *Quercus* forests in the Neotropics, and the possible history of the group, all of the above life history factors must be considered. Although less well-known taxonomically, the oaks of the Mexican and Central American forests appear to exhibit similar patterns of morphological variation and life history as do oaks in the forests of the USA and Europe, which have been more intensively studied. That said, there also clearly are differences in the Neotropical species of *Quercus* in terms of life history factors. The most obvious of these is a less precise seasonality in Neotropical oaks.

1.3 Distribution and Species Diversity

On the American continent, species of the genus *Quercus* (oak) occur in Canada, the USA, Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama and Colombia. Figure 1.1 shows the distribution of *Quercus* in the Americas.

Estimates of species diversity within new World *Quercus* have changed over the years, but we now have a fairly accurate estimate based on recent floras and broad treatments (Nixon 1993a, 1997b, 2003), and work in progress (Flora Mesoamericana, Nixon, unpublished data). The overall number of species in the New World, including Latin America, the United States and Canada, is probably around 220 species. Estimates of the total number of oak species that occur, along with endemics, in American countries in which *Quercus* is naturally found are as follows: four in Canada, 91 in the USA, one in Cuba, 160–165 in Mexico, nine in Belize, 25–26 in Guatemala, 8–10 in El Salvador, 14–15 in Honduras, 14 in Nicaragua, 14 in Costa Rica, 12 in Panama, and one (*Quercus humboldtii*) in Colombia.

The greatest species diversity for the genus *Quercus* in the New World occurs in the mountains of southern Mexico (Nixon 1993a). Another center of diversity occurs in the southeastern United States, but not particularly associated with the Appalachian Mountains. The Rocky Mountain region is depauperate in oak species, as is the Pacific Northwest.

Traveling southeast from Mexico into Central America, one notes a gradual reduction of oak species diversity. Eventually, when one reaches Colombia, there is a single species of oak (*Q. humboldtii*, subdivided into 2–3 species by some authors; see Chap. 11).

Seasonality in the temperate and subtropical oaks, including those of North America and Europe, results in relatively consistent patterns of flowering and fruit production. Most temperate species have a characteristic flowering time in the spring months (usually somewhere between February and

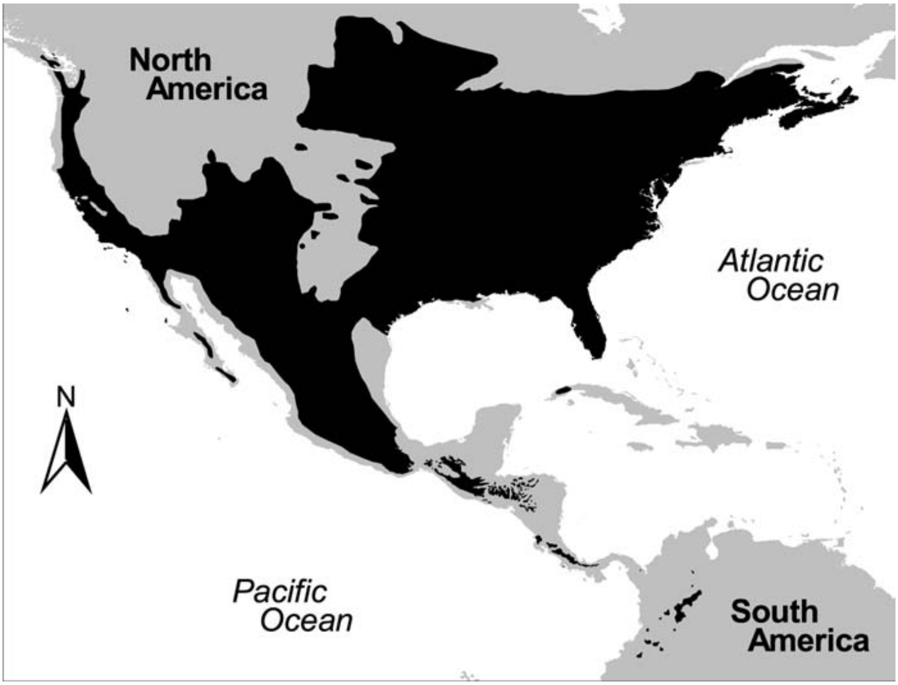

Fig. 1.1. Map showing the outer limits of the distribution of oak (genus *Quercus*) on the American continent. The genus ranges from southern Canada to southern Colombia, and is found in the northwest corner of Cuba. In Mesoamerica and Colombia, it is found mainly in mountainous areas above 1,000 m elevation. Map prepared by Marco V. Castro Campos at The Nature Conservancy

June, depending on the species and latitude), and a fairly fixed fall fruit production period – acorns fall mostly in the months of September–November, with the greatest production in October. This is true throughout much of montane Mexico as well, with most species flowering in March–April, and producing fruit in October–November.

The tropical and montane tropical oaks from southern Mexico to Colombia, however, present a different pattern of flowering and fruit production, which in some species is less predictable. The majority of oak species in the Mesoamerican region flower in the 'dry season', varying from October to February, with a peak fruiting time during the rainy season in June–July. To date, there have been very few studies of the exact phenology of these tropical species (Céspedes 1991, Chap. 19), and even less is known on the mechanisms by which flowering synchronization might occur. In Costa Rica, Céspedes (1991) observed during a year of observation a strong periodicity in leaf flushing, leaf fall, flowering and fruiting in *Quercus seemannii* at 1,700 m altitude. He noted that leaf fall occurred practically all year around, but was more