Comparative Ecology of North-Central Florida Oaks

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A critical issue in ecology is understanding the forces that give rise to biological diversity. Central to this question has been a quest to explain the patterns of species distributions and abundance across the landscape (Huston 1994) and to determine whether species specialize to partition the environment, or whether distributions are the result of predominantly stochastic processes (Diamond and Case 1986; Brokaw and Busing 2000). The complexity of ecology has lead to the inclusion of multiple mechanisms for explaining species distributions and the forces leading to biological diversity and species coexistence (Ashton 1998). If species do specialize to partition their environment, we would expect to be able to identify predictable functional traits that allow certain species to succeed under one set of environmental conditions and other species to succeed under contrasting environmental conditions. Indeed, a central goal of many ecological studies has been to explain patterns of species distributions based on life history and functional traits (Chapin *et al.* 1993; Reich *et al.* 1999). Previous empirical and theoretical work in this area has given rise to expectations about how such traits vary across environmental gradients (Tilman 1988; Goldberg 1997).

I investigated these issues within a system of sympatric oak species in northern central Florida. Seventeen species of oaks occur here (see Table 1), making it one of the regions of the highest oak species diversity in the United States (Burns and Honkala 1990; Platt and Schwartz 1990; Nelson 1994). Globally, the co-presence of this number of congeners is a rare phenomenon. These oaks are phenotypically and ecologically diverse and can be identified as discrete morphotypes, which contrast starkly in morphology, stature, and leaf phenology (Kurz and Godfrey 1962; Nixon 1997). Floridian species in the genus *Quercus* represent three phylogenetic lineages: section *Lobatae* or red oaks, section *Quercus sensu stricto* or white oaks in the strict sense, and section *Quercus* subsection *Virentes* or live oaks (Nixon 1997; Manos *et al.* 1999).

The co-presence of so many closely related species is particularly intriguing given the lack of major elevational changes in Florida and the predominance of relatively barren, sandy soils. Upon closer examination of the landscape, one finds that there is a vast system of above and below-ground rivers in Florida, which gives rise to a strong gradient in soil moisture regimes between riparian zones and xeric uplands. There is also a more subtle environmental gradient that arises from Florida's karst topography, in which limestone bedrock is overlain with a clay layer and then by sand. Underground rivers can erode the bedrock, causing the soil surface to cave in, resulting in the formation of ravines. Within these ravines, deep sands may give way to exposed clay with standing water often occurring at the bottom as the water table is approached. Across this topography, small changes in elevation can lead to large changes in water availability, accompanied by changes in soil fertility (Fig. 1).

Fire is another critical environmental factor. Due to the high frequency of electrical storms in Florida, lightning is more frequent in this region than anywhere else in North America, resulting in frequent fires (Chen and

contd. on pg. 26

Table 1 Species list and habitat distribution

Species	Breadth of distribution across habitat types	Soil moisture regime
	Section *Lobatae*	
Q. falcata	Narrow	Dry
Q. hemispherica	Broad	Dry to Moderately wet
Q. incana	Narrow	Dry
Q. laurifolia	Narrow	Wet
Q. laevis	Narrow	Dry
Q. myrtifolia	Narrow	Dry
Q. nigra	Broad	Moderately dry to Wet
Q. shumardii	Narrow	Moderately wet
Q. pumila	Narrow	Intermediate
	Section *Quercus s.s.*	
Q. stellata	Moderate	Intermediate
Q. margaretta	Narrow	Dry
Q. michauxii	Moderate	Intermediate to Wet
Q. austrina	Narrow	Moderately dry
Q. chapmanii	Narrow	Dry
	Section *Quercus*, subsection *Virentes*	
Q. geminata	Narrow to Moderate	Dry to Moderately dry
Q. minima	Narrow	Intermediate
Q. virginiana	Broad	Dry to Wet

North-Central Florida Oaks . . .

contd. from pg. 25

Gerber 1990). The dynamics of the fire regime can lead to contrasting vegetation communities (Myers and Ewel 1990). These gradients in soil moisture, nutrients, and fire dynamics create spatial and temporal heterogeneity and allow the possibility that oak species are partitioning the landscape along multiple environmental axes.

In this system, the oaks do appear to partition their environment with some species, such as *Q. laurifolia, Q. shumardii* and *Q. michauxii,* occurring at the wet end of the soil moisture gradient, and others, such as *Q. margaretta, Q. leavis, Q. myrtifolia, Q. chapmanii* occurring at the xeric end. Still other species, such as *Q. hemispherica, Q. virginiana*, and *Q. nigra* can occur both in wet and dry sites. There are clear differences among species in the breadth of their distributions across soil moisture gradients, with some species specializing for particular soil moisture regimes and soil types, and other species having broad distributions across the land-

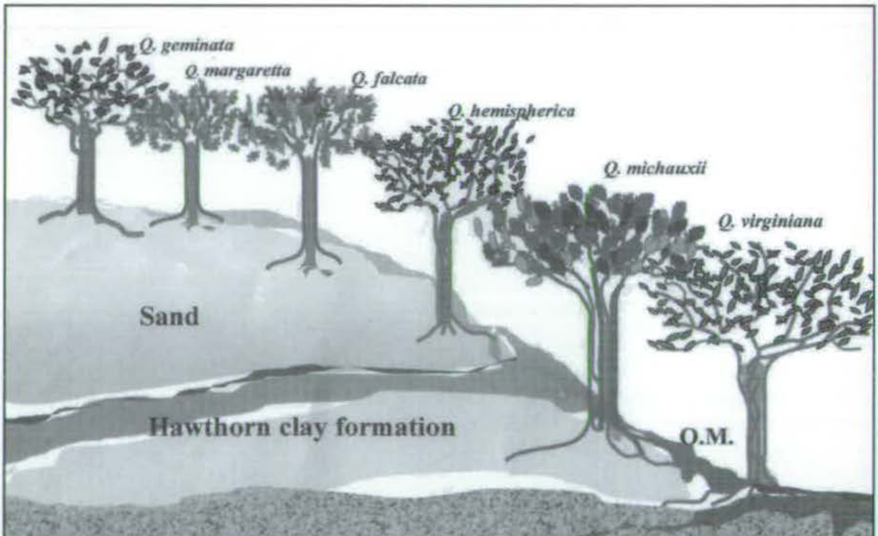

Figure 1. *Stylized diagram of the distribution of species along a gradient from uplands to wetlands. The scenario depicts, in particular, the change in oak species from sandy uplands to ravine bottoms where the water table reaches the surface, a pattern which can easily be seen at San Felasco Hammock State Preserve in Alachua Co., Florida.*

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Figure 2. *Quercus hemispherica probably exhibits the broadest ecological amplitude of any oak species in north-central Florida.*

scape and found in many different habitat types (see Table 1). *Q. hemispherica* is among the broadest niched species in this region.

Fire dynamics greatly influence the landscape and the distribution of species. Both fire frequency and fire intensity are important factors that influence which species are promoted or discouraged in particular communities (Myers 1990). Several oak species, including *Q. myrtifolia, Q. chapmanii,* and *Q. geminata* can tolerate intense fires that destroy a large percentage of their above-ground biomass. These species allocate a large proportion of their total biomass below ground and grow clonally. They also have been shown to root graft and share below-ground resources among individuals (Guerin 1993). These traits allow rapid regrowth after fire. Other oak species, such as *Q. laevis, Q. margaretta, Q. incana* are promoted by frequent fires, which are less intense, rarely reaching the crown. These species tend to have thick bark as juveniles, allowing them to survive ground fires. In addition, there are two runner oaks in this region of Florida, *Q. pumila* and *Q. minima*, which are found in moderately xeric to mesic habitats and thought to be highly fire-adapted. They both have underground stems and their aboveground stems may reach less than a meter in *Q. pumila* and a maximum of 2 or 3 meters in *Q. minima*. These species are found in seepage areas where soil nutrients may be low, but water is available (Kurz and Godfrey 1962).

That some species are found in more mesic environments and others in more xeric environ-

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North-Central Florida Oaks . . .

contd. from pg. 27

ments appears to be paralleled by several traits important for water transport. Branches of species in mesic to hydric conditions have higher maximum hydraulic conductances than those of species generally found in xeric conditions. These species also have higher growth rates, higher leaf area per shoot, and higher transpirational water loss per sapwood area (Cavender-Bares and Holbrook, submitted).

Often, but not always, increases in soil moisture are paralleled by increases in soil richness. Species growing in richer, more mesic soils tend to have taller maximum heights, larger acorn sizes, and higher absolute growth rates as seedlings. Such attributes may give plants an advantage in accessing light in these rich habitats where productivity is high and competition for light in the understory is intense (Tilman 1988). Both fire frequency and intensity also tend to be low in these types of habitats.

Phenology varies among these 17 species as some are deciduous, leafing out in the spring and senescing in the fall, while others maintain a foliated canopy year-round. Still others show intermediate behavior, dropping their leaves partway through the winter. These differences in phenological patterns may promote the co-occurrence of multiple oaks in relatively close proximity if they allow for temporal separation in resource acquisition.

In this system, species from distinct phylogenetic lineages are more likely to be found in the same habitat than species from the same phylogenetic lineage. Hence, there is a tendency for closely related species to be found in contrasting habitats where they are less likely to compete with each other. More distantly related species may be more likely to co-habitate, and this may be an important factor in allowing congeners to occur in close geographic quarters (Mohler 1990). One such mechanism promoting co-occurrence of oaks from different phylogenetic lineages may be related to the timing of acorn maturation in red oaks versus white oaks. Acorns generally take two years to mature in red oaks and only one year in white oaks. If a hard frost kills the flowers in a particular spring, this will prevent white oaks from developing acorns and dropping them in the fall of that year. Red oaks are still likely to have viable acorns that year, but the following year's crop will be affected. Hence, a staggering of seedling regeneration could occur in which establishment of red oak seedlings are promoted in some years and white oak seedlings are promoted in other years. Mechanism such as this may reduce competition between red and white oaks and increase their likelihood of co-occurrence.

In summary, the North-Central Florida landscape provides considerable environmental heterogeneity in soil moisture availability, nutrient availability and fire regime to allow for species to partition their environment and occupy contrasting microhabitats. Traits of species in terms of water relations, growth, and fire tolerance fit well with their separation into different habitats. However, several species are generalist and may grow in a number of habitats. The fact that more distantly related species are more likely to be found together may reduce competition among very similar species and ultimately allow more oak species to occur together.

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