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Phylogenetic Overdispersion in Floridian Oak Communities

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abstract: Closely related species that occur together in communities and experience similar environmental conditions are likely to share phenotypic traits because of the process of environmental filtering. At the same time, species that are too similar are unlikely to co-occur because of competitive exclusion. In an effort to explain the coexistence of 17 oak species within forest communities in North Central Florida, we examined correlations between the phylogenetic relatedness of oak species, their degree of co-occurrence within communities and niche overlap across environmental gradients, and their similarity in ecophysiological and life-history traits. We show that the oaks are phylogenetically overdispersed because co-occurring species are more distantly related than expected by chance, and oaks within the same clade show less niche overlap than expected. Hence, communities are more likely to include members of both the red oak and the white + live oak clades than only members of one clade. This pattern of phylogenetic overdispersion arises because traits important for habitat specialization show evolutionary convergence. We hypothesize further that certain conserved traits permit coexistence of distantly related congeners. These results provide an explanation for how oak diversity is maintained at the community level in North Central Florida.

Keywords: phylogenetic structure of communities, null models, ecological filtering, species interactions, conserved and convergent trait evolution, *Quercus.*

A critical challenge in community ecology is to understand how the attributes of species influence community assembly and how these attributes, and hence community composition, depend on the evolutionary lability of phenotypic traits. There are two central processes involved in the assembly of communities: filtering of species that can persist within a community on the basis of their tolerance of the abiotic environment (Weiher and Keddy 1995; Weiher et al. 1998) and competitive interactions among species that limit their long-term coexistence (Gause 1934; Elton 1946; MacArthur and Levins 1967; Chesson 1991; Leibold 1998). These two processes make opposite predictions about the phenotypic similarity and phylogenetic relatedness of co-occurring species (fig. 1; Tofts and Silvertown 2000; Webb 2000). If closely related species share similar physiological limitations (fig. 1*B*) and exhibit evolutionary niche conservatism, the former process, environmental filtering, will tend to cause closely related species to co-occur; this pattern can be termed “phylogenetic clustering”[1] (fig. 1*A*). In accord with this prediction, several previous studies have shown that related species are more likely to co-occur than expected by chance (Tofts and Silvertown 2000; Webb 2000). However, competitive exclusion should limit the coexistence of closely related species if species share limiting resources, leading to the opposite pattern of phylogenetic overdispersion (fig. 1*A*). Recently, Losos et al. (2003) showed that when co-occurring species have evolved in sympatry, as in the case of Caribbean lizard communities, niche conservatism cannot be assumed. A long history of competitive interactions apparently caused evolutionary divergence in species niches, resulting in phylogenetic overdispersion. Phylogenetic overdispersion has

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[1] Here we use the terms “clustering” and “overdispersion.” While clustering is intuitive, overdispersion should be equated with evenness. Previously, two of us have used the terms “attraction” and “repulsion” to describe the same patterns (Webb et al. 2002; Cavender-Bares and Wilczek 2003). However, these terms imply processes. The terms “clustering” and “overdispersion” are free from implications about the processes by which the patterns arose, and these patterns can be directly tested for using the statistical methods presented.

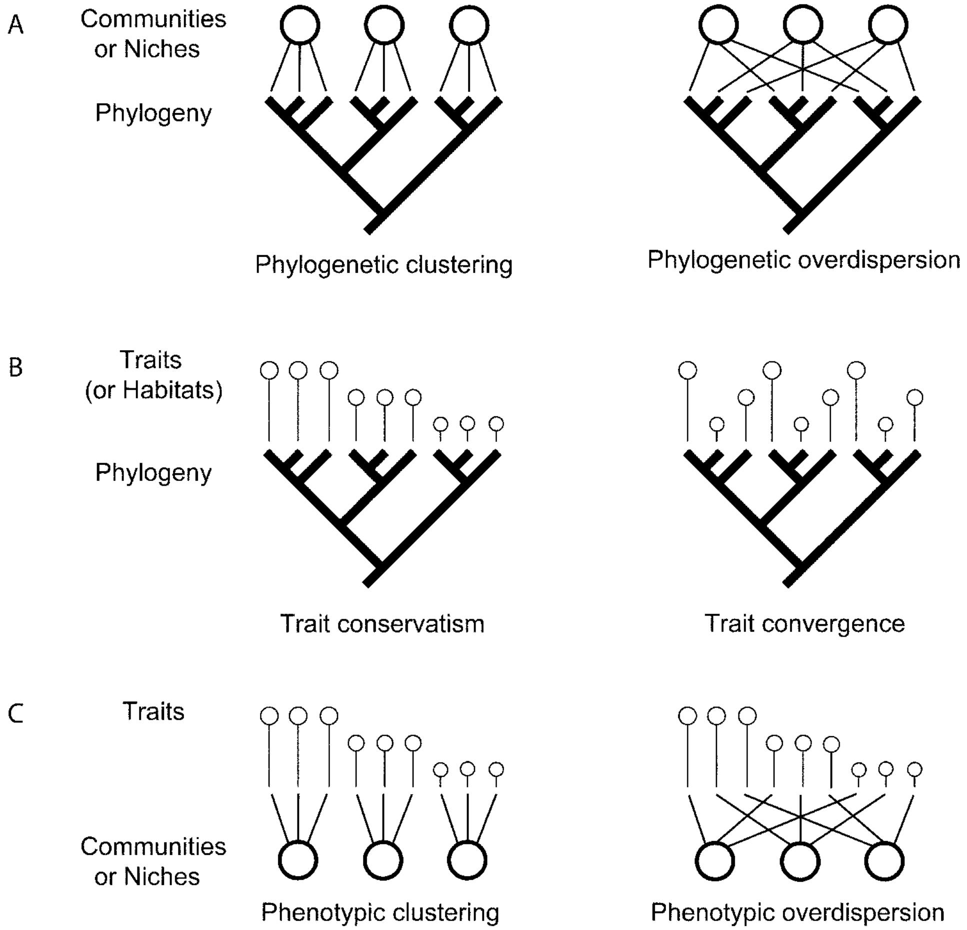


Figure 1: *A*, Phylogenetic structure of communities or niches can show patterns of clustering (*left*) at one end of the spectrum or overdispersion (*right*) at the other end of the spectrum. *B*, Evolution of species traits may show patterns of conservatism (*left*) or convergence (*right*). The interaction of phenotypes of sympatric species (competition) and the environmental tolerances of phenotypes (filtering) determine the phenotypic structure of communities. *C*, Environmental filtering can cause trait values of species within communities to be more similar than expected (phenotypic clustering; *left*). Competitive interactions may cause traits of species to be more different than expected (phenotypic overdispersion; *right*). Metrics to test for these patterns are presented in the study.

yet to be demonstrated using phylogenetic analysis in plant communities.

In natural communities, both environmental filtering and competitive interactions are occurring (Ackerly 2003); hence, as characters evolve along phylogenetic lineages, some may confer increased environmental tolerance (filtering), while others may reduce competition among species. The combination of species traits and their evolutionary lability produces the phylogenetic structure that is observed within communities (fig. 1; Webb et al. 2002).

The diverse oak forests of North Central Florida, which are dominated by multiple species of a single genus, present a challenge to the principle of competitive exclusion and provide an important system in which to examine the mechanisms that may give rise to phylogenetic structure within communities and promote species coexistence. The high diversity of oak species in Florida can be explained, in part, by habitat differentiation at the landscape level, with species occurring in three major community types (hammock, sandhill, and scrub) differentiated by contrasting fire regimes and/or soil moisture and soil fertility regimes (Cavender-Bares et al., in press). However, at small spatial scales, up to six species of oaks (median of three) still occur within a single 0.10-ha plot (see fig. A1 in the online edition of the *American Naturalist*). It has previously been observed that co-occurring oaks are more likely to be from different sections of the genus than from the same section (Whittaker 1969; Mohler 1990). Here we examine the phylogenetic structure of oak communities in North Central Florida, where 17 species of oaks co-occur, to test the hypothesis that co-occurring oak species are more distantly related than expected (phylogenetic overdispersion; fig. 1*A*) because of factors limiting the coexistence of closely related species. We then examine the evolutionary lability of species functional traits (fig. 1*B*) and test whether the similarity of individual traits is related to species co-occurrence within communities (fig. 1*C*). This provides us with a framework for explaining the phylogenetic structure of oak forests (fig. 2). If conserved traits are clustered within communities and these traits are adaptively linked to environmental conditions in those communities, this would explain a pattern of phylogenetic clustering (fig. 2). In contrast, if convergent traits are clustered (again because of environmental filtering) and/or conserved traits are overdispersed (because of species interactions), this would explain the hypothesized pattern of phylogenetic overdispersion (fig. 2). Where individual functional traits show opposing patterns, we can begin to hone in on the precise mechanisms by which phylogenetic structure arises within communities and ultimately to understand how diversity is maintained within them.

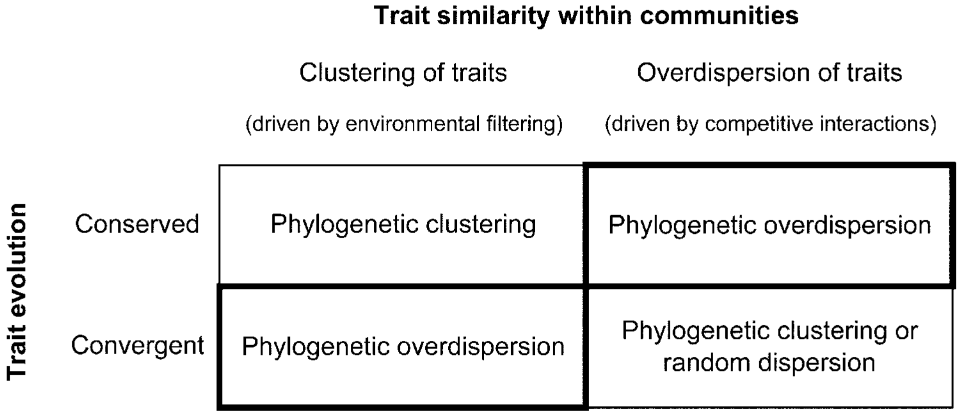
In this study, we combine four different kinds of data (phylogenetic, spatial, phenotypic, and environmental) and develop a series of metrics for examining the phylogenetic and phenotypic structure of community assemblages, outlined in figure 1. We also examine the phylogenetic structure of communities at various phylogenetic scales, since clustering or overdispersion may occur at any scale (Silvertown et al. 2001). Null models assuming random spatial distributions (with constraints) or randomized phylogenetic relationships between species are used to examine the departure of observed from expected patterns.

Methods

Phylogenetic Analysis

The phylogeny of *Quercus*, with >400 species, is complex and has been studied in considerable detail (Nixon and Crepet 1989; Manos et al. 1999, 2001; Manos and Stanford 2001). For this study, it was necessary to estimate the phylogenetic relationships among the 17 Floridian oak species occurring in our study system. We sequenced the internal transcribed spacers (ITS) and 5.8S coding sequence of nuclear ribosomal DNA (Coleman and Mai 1997) and estimated the phylogeny using maximum parsimony and maximum likelihood.

Voucher specimens for the 17 Florida oak species, including Universal Transverse Mercator coordinates for source tree locations, are held at the Harvard University Herbaria. Identification of species was based on the classification of Kurz and Godfrey (1962) and Nixon et al. (1997). Genomic DNA was isolated from fresh leaf material for each species and extracted using the DNeasy Plant Mini Kit (QIAGEN, Valencia, Calif.). The ITS region was amplified using polymerase chain reactions with flanking primers ITS.LEU and ITS.4 plus internal primers ITS.2 and ITS.3B (Baum et al. 1994). The cleaned, quantified products were sequenced using the ABI Prism Big Dye Terminator Cycle Sequencing Reaction Kit (PE Applied Biosystems, Foster City, Calif.) and then run on an ABI



		Trait similarity within communities	
		Clustering of traits (driven by environmental filtering)	Overdispersion of traits (driven by competitive interactions)
Trait evolution	Conserved	Phylogenetic clustering	Phylogenetic overdispersion
	Convergent	Phylogenetic overdispersion	Phylogenetic clustering or random dispersion

Figure 2: Two ecological forces give rise to opposite expectations about the similarity of traits within communities. If environmental filtering dominates, co-occurring species sharing the same abiotic environment should be more similar than expected (clustering of traits). If competitive interactions dominate, co-occurring species should be phenotypically less similar than expected (overdispersion of traits). Which ecological force can be invoked to explain a given phylogenetic structure depends on whether trait evolution is conserved or convergent. In order for a community to show phylogenetic overdispersion, competitive interactions must cause the overdispersion of conserved traits or environmental filtering must cause the clustering of convergent traits (or both). Figure adapted from Webb et al. (2002).

Model 377 automated DNA sequencer using Long Ranger gels (FMC Bioproducts, Rockland, Maine). Contigs were assembled using Sequencher version 3.0 (Gene Codes, Ann Arbor, Mich.). The sequencing strategy allowed the entire region to be sequenced in both directions except for close to the priming sites. In addition to the 17 individuals analyzed here, we sequenced two to four additional representatives of these species as a check for problems of hybridization or cryptic variation. These additional accessions showed little relevant intraspecific variation in ITS, and species monophyly was not strongly contradicted (data not shown), except for one individual of *Quercus virginiana* and two of *Q. geminata* for which a second class of ITS sequences was found. These sequences fell in an anomalous position in preliminary phylogenetic analyses (based on information from Manos et al. 1999) and could represent sequences acquired through introgression (Whittemore and Schaal 1991) or ITS pseudogenes (Buckler et al. 1997). These anomalous sequences were not analyzed further. We used the original single sequence obtained for each species to obtain a phylogenetic estimate with branch lengths to be used for comparative analyses. GenBank accession numbers for these sequences are AY456162–AY456178. Species, authorities, herbarium voucher numbers, and GenBank accession numbers are listed for each species in data file 1 (available for download in the online edition of the *American Naturalist*).

Phylogenetic analysis was conducted using PAUP 4.0b7 (Swofford 2001). After alignment, we conducted parsimony analysis of the 17 species of interest and found four most parsimonious trees using 100 replicates of random taxon addition with tree bisection reconnection (TBR) branch swapping. To evaluate internal support for the resultant topology, we analyzed 100 bootstrap replicates using simple addition sequence TBR searches and obtained bootstrap proportions for each clade. To determine the correct rooting of Floridian taxa and to see whether there was an effect of the addition of further taxa, we also analyzed a 37-taxon matrix that included 20 published oak sequences (data file 2, available for download in the online edition of the *American Naturalist*). An initial search was conducted using 100 replicates of random taxon addition with TBR branch swapping but keeping no more than 10 trees per replicate. We found that this search accurately represented the phylogenetic structure in the pool of most parsimonious trees by conducting a second search with the same settings but constrained to consider only trees that were incompatible with the strict consensus from the previous search (Catalan et al. 1997).

Branch Length Estimation

Branch lengths were calculated on all four most parsimonious trees using two different models of evolution (Swofford 2001): HKY, maximum likelihood estimation of branch lengths based on the HKY85 model of evolution with gamma-distributed rate heterogeneity among sites (transition-transversion rate and gamma shape parameter estimated from the data), and HKY + clock, which is similar to HKY except with a molecular clock enforced and the tree rooted between the red oaks and the remaining taxa as suggested by the 37-taxon analysis and by Manos et al. (1999). Sites with missing or ambiguous data were deleted. Likelihood ratio tests (Huelsenbeck and Rannala 1997) show that the clock model could not be rejected; we therefore used HKY + clock branch lengths in subsequent analyses.

Field Sampling for Spatial and Environmental Data Collection

Distributions of plant species in North Central Florida, including the oaks that dominate the forest communities, are strongly influenced by three environmental factors: soil moisture, soil fertility, and fire regimes (Monk 1968; Whittaker 1969; Ewel 1990; Mohler 1990; Myers and Ewel 1990; Jackson et al. 1999). These three factors are correlated with each other, and three primary community types are recognized in the landscape: sandhill, hammock, and scrub. Sandhill communities are xeric, open woodlands with deep, sandy soil. Fire frequency is high (1–15 yr) but severity is low, rarely extending into the crowns of trees. Scrub communities are characterized as dense thickets, with xeric sandy soils and infrequent fires (on the order of every 50 yr) of high severity that tend to destroy the aboveground biomass. Hammock communities include mesic or hydric temperate hardwood forests with richer soils and low frequency fires of low or unpredictable severity (Kurz 1942; Kurz and Godfrey 1962; Ewel 1990; Myers 1990; Platt and Schwartz 1990). Community affiliations for species are as follows: sandhill: *Q. incana*, *Q. margaretta*, *Q. laevis*, and *Q. falcata*; hammock: *Q. virginiana*, *Q. austrina*, *Q. stellata*, *Q. nigra*, *Q. hemispherica*, *Q. laurifolia*, *Q. shumardii*, and *Q. michauxii*; scrub: *Q. myrtifolia*, *Q. chapmanii*, *Q. geminata*, *Q. pumila*, and *Q. minima* (Kurz and Godfrey 1962; Cavender-Bares et al., in press).

For this study, quantitative data on vegetation and soil variables were collected from randomly established 0.10-ha (20 × 50 m) plots in three state preserves in northern central Florida. The preserves included San Felasco Hammock State Preserve, a 2,803-ha park in Alachua County; Ichetucknee Spring State Park, a 921-ha park bridging Columbia and Suwanee counties and bisected by the Ichetucknee river; and Manatee Springs State Park, a 960-ha park abutting the Suwanee river in Levy county. These parks represent natural areas with minimal recent disturbance, including large areas undeveloped by European settlers. The natural fire regime was suppressed within the last 50 yr, although a controlled fire regime has been imposed in the last 20 yr. Random plots were established in each park for a total of 74 plots. Plots were excluded from road edges and the northern region of San Felasco, which had experienced fairly recent agricultural and logging disturbances. Within each plot, the diameter at breast height (dbh) of each oak tree more than 1.3 m in height was measured for calculation of basal area. The presence/absence of oaks and other woody species was also recorded for each of the plots. Median oak diversity at the plot level was three, with a range from one to six species (fig. A1). Within four subplots of each plot, soil samples to 10-cm depth were analyzed for organic matter content, calcium content, pH, exchangeable nitrate and ammonium, labile phosphorus, potassium, and magnesium at the soil testing laboratory at the University of Florida. Soil moisture to 1-m depth was repeatedly measured using time domain reflectometry in four subplots of each plot over a 14-mo period during both wet and dry cycles, as described in Cavender-Bares and Holbrook (2001). Species habitat preferences for soil factors were determined from species distributions across the three state preserves using mean values of soil moisture (averaged for each plot over the 14-mo period) and soil fertility, weighted by basal area of species within plots (Jongman et al. 1995).

Measurements of Traits

A suite of functional traits was measured on mature trees across the range of their distributions in the field, primarily at San Felasco Hammock State Preserve, or on seedlings grown under common conditions in glasshouse facilities at Harvard University. Traits examined included leaf life span (d), xylem embolism due to freezing (percent loss of hydraulic conductivity after freezing), wood density (g cm^{-3}), vessel diameters of first- and second-year wood of sunlit branches (μm), hydraulically weighted vessel diameters (which takes into account the distribution of different vessel diameters and their contribution to xylem transport; Sperry et al. 1994), sapling outer bark thickness (cm), asymptotic height (m), radial growth rate (mm yr^{-1}), rhizome resprouting potential (an index based on the ability to spread clonally and resprout from underground rhizomes and roots), native embolism (percent loss of hydraulic conductivity during a seasonal drought in July 1999), maximum hydraulic conductivity (kg H_2O m MPa s^{-1}), whole shoot transpiration normalized by sapwood area (mmol H_2O m^{-2} s^{-1}), and acorn maturation time (yr). Traits measured on seedlings included relative growth rate (g g^{-1} d^{-1}), absolute growth rate (g yr^{-1}), and whole canopy transpiration rate (mmol H_2O s^{-1} $plant^{-1}$). Gas exchange measurements were carried out with a licor 6400 (Licor, Lincoln, Nebr.) on sunlit leaves under saturating light conditions (2,000 μmol) using an LED attachment. Hydraulic conductance was measured using the Sperry method (1988). Methods for measuring vessel diameters and embolism due to freezing are explained in Cavender-Bares and Holbrook (2001).

Asymptotic tree height, a measure of average maximal height, was estimated by measuring height and dbh of 50–100 individuals of all sizes for each species and fitting an exponential function to the data as described by Thomas and Bazzaz (1999). Rhizome resprouting potential was determined by a rank assigned to each species on the basis of seedling experiments, observations in the field, and published sources (Webber 1935; Kurz and Godfrey 1962; Burns and Honkala 1990; Guerin 1993; Menges and Kohfeldt 1995; Nixon et al. 1997; Greenberg and Simons 1999) according to the following criteria: no resprouting from rhizomes or roots; resprouting from rhizomes possible but rare; occasional vegetative reproduction from rhizomes and clonal spreading in small patches; considerable sprouting from roots and underground runners almost always present, including clonal spreading and dome formation. Sapling outer bark thickness was measured adapting methods described by Adams and Jackson (1995) and Jackson et al. (1999). Data for five species (*Q. stellata*, *Q. virginiana*, *Q. laurifolia*, *Q. shumardii*, and *Q. michauxii*) were taken from Jackson et al. (1999). Acorn maturation times (number of years for the acorns to develop to maturity) are from Nixon et al. (1997).

Measurement of all other leaf level and whole plant traits examined in this study were carried out on six to 10 mature trees of each species on stems or leaves of sunlit branches in order to control for light level. Tree canopies were accessed using an aerial lift or scaffolding towers. Leaf life span was calculated from leaf birth and death dates monitored monthly over 2 yr on three branches per tree using the primary cohort of leaves that emerges in spring. Radial growth increment, a measure of absolute growth rate, was calculated from tree ring widths from tree cores of mature trees. We restricted measurements of tree ring widths to the previous 10 yr of growth to ensure that measurements were made only for years when the canopies were exposed.

Seedling traits were measured on a subset of nine species, including *Q. falcata*, *Q. geminata*, *Q. hemispherica*, *Q. laevis*, *Q. margaretta*, *Q. michauxii*, *Q. myrtifolia*, *Q. nigra*, and *Q. virginiana*, grown under common conditions in a glasshouse at Harvard University. Seeds were collected in Florida in the fall of 1997, germinated in trays the following spring, and transplanted to pots in a mixture of sand, peat, and vermiculite in the fall of 1998. Transplanted seedlings, approximately 25 plants per species, were given 18 g of slow-release fertilizer. Gas exchange measurements were carried out the following summer. Absolute growth rate was determined by dry biomass after one complete year following transplanting from germination trays to pots. Relative growth rate (RGR) was calculated as follows:

$$\mathrm{RGR} = \frac{\log_e(M_{\mathrm{final}}) - \log_e(M_{\mathrm{initial}})}{T_{\mathrm{final}} - T_{\mathrm{initial}}}, \tag{1}$$

where M_{final} and M_{initial} are dry biomass at the time of harvest (T_{final}) and the time of transplanting (T_{initial}) from germination trays into pots (Hunt 1982). The M_{initial} was determined from allometric equations determined from measurements of leaf size, leaf number, stem diameter, and plant height from at least 30 additional seedlings per species that were harvested, dried, and weighed (data file 3, available for download in the online edition of the *American Naturalist*). Seedling whole plant transpiration rates were calculated by multiplying mean maximum transpiration rates per species by the average leaf surface area per species.

Tests for Environmental Filtering

One method for examining environmental filtering is to determine whether there are correlations between species traits and their environments (e.g., Ackerly et al. 2002). The use of independent contrasts (Felsenstein 1985; Garland et al. 1991; Ackerly 1999) tests for correlated evolution in traits with respect to aspects of their habitats. We calculated independent contrasts to determine whether functional traits showed correlated evolution with habitat preferences, including soil moisture, soil fertility, and fire regime. Contrasts were standardized by branch lengths (Garland et al. 1992). The use of different branch length estimations did not change the correlations in any meaningful way, and for brevity, only contrast correlations using HKY + clock branch lengths are presented. Soil fertility is reported as exchangeable nitrate N + ammonium N (mg kg^{-1}); this measure is highly correlated with other soil fertility factors (Cavender-Bares et al., in press). Fire regime is given in two ways. First, we report the fire regime in terms of a ranked index of fire return interval for individual species provided by Jackson et al. (1999), which does not include the five scrub species (listed previously). The ranking is as follows in order of increasing fire return interval (decreasing fire frequency): (1) *Q. incana*, *Q. laevis*, *Q. margaretta*; (2) *Q. falcata*, *Q. stellata*; (3) *Q. austrina*, *Q. hemispherica*; (4) *Q. shumardii*; and (5) *Q. laurifolia*, *Q. michauxii*, *Q. nigra*, *Q. virginiana*. Second, there are three broadly defined fire regimes that occur in oak-dominated forests that follow a gradient of fire severity and correspond to the three community types described previously: first, low or unpredictable severity and very low frequency fires (100–1,000 yr) that occur in hammock areas of high soil moisture and rapid decomposition; second, intermediate severity and high frequency fires (every 1–15 yr) that rarely extend into the crown and occur in xeric sandhill regions (these are ignited by frequent lightning and facilitated by long leaf pine [*Pinus palustris*] and understory grasses promoted by an open canopy); and third, high severity fires that occur with predictable frequency (on the order of every 50 yr) but destroy the aboveground biomass, facilitated by fire resistance of the vegetation in scrub communities until fuel build-up is high. Independent contrast calculations were performed using the CACTUS computer program (Schwilk 1999) and were tested over four tree topologies.

Tests for Phylogenetic Overdispersion

Co-occurrence within Communities. To test for phylogenetic overdispersion in communities, we determined whether there was a significant correlation between the phylogenetic distance of pairs of taxa and their degree of co-occurrence within plots. The phylogenetic distance is the sum of the estimated lengths of all intervening branches between two species on the phylogeny. Pairwise values of co-occurrence were calculated using a co-occurrence index (CI) based on proportional similarity (Schoener 1970): $\mathrm{CI}_{ih} = 1 - 0.5 \times \sum |p_{ij} - p_{hj}|$, where CI_{ih} is the co-occurrence of species i and h and p_{ij} is the proportion of total basal area or the proportion of occurrences of the ith species in the jth plot. The correlation coefficient obtained from the test was compared with three null models (see below).

Niche Overlap. A similar test was done to examine the phylogenetic relationships of species in relation to their field distribution along a soil moisture gradient. We correlated pairwise values of niche overlap with phylogenetic distance and compared the correlation coefficient with an expected value determined from the three null models. The niche structure of these 17 oak species was examined by using soil moisture as the primary niche axis. Niche overlap was computed for seven soil moisture levels, each spanning a change of 5% soil moisture, on the basis of Pianka's species overlap index (Pianka 1973) using basal area as the raw data matrix according to the following equation:

$$O_{jk} = O_{kj} = \frac{\sum_i^n E_{ij}E_{ik}}{\sqrt{\sum_i^n (E_{ij}^2) \sum_i^n (E_{ik}^2)}},$$

where O_{jk} is the overlap of species j on species k, i is the soil moisture level, n is the number of levels ($n = 7$), and E_{ij} is the proportion of basal area or occurrences of species j in level i divided by the number of plots that fall within level i. Soil moisture levels were assigned the following ranges: <7%, 7%–12%, 12%–17%, 17%–22%, 22%–27%, 27%–32%, and >32%. Bin width and number can influence the outcome of such analyses. We chose the minimum number of bins that gave good resolution of species niche structure but minimized the number of empty bins. A sensitivity analysis showed that the analyses were robust to changes in bin width and that increasing the number of bins up to 15 did not change the results. Whether the first and last bins were open-ended or not did not influence the results. Basal area was standardized so that it summed to 1 for each taxon across all niche bins.

Null Models. For null model 1, species were randomized 1,000 times across the phylogeny using a program written in Visual Basic (available on request) to shuffle the phylogenetic distance scores. In null models 2 and 3, phylogenetic distances were kept fixed, but the spatial distribution or niche structure of species was randomized. In null model 2, the basal area of each species across plots was randomized by reshuffling raw data values across plots but constraining the total basal area per species. Null model 3 used presence/absence data instead of basal area and constrained both total occurrences per species as well as total number of species per plot. The null model for the presence/absence data may be the most realistic biologically because it constrains both species abundances and plot diversity levels (Gotelli and Graves 1996). However, presence/absence data provide a lower degree of resolution for the distributions of species than basal area because differences in relative abundance within plots are not considered. A null model that constrains total basal area per species and plot would probably be impossible to construct and was not attempted in this study.

Distribution data were randomized using the knights tour algorithm (Gotelli and Entsminger 2001*b*) using a program written in Visual Basic or by the sequential swap method in the null model software EcoSim (Gotelli and Entsminger 2001*a*). In the latter case, randomized matrices were saved and read by a program written in Visual Basic that calculated co-occurrence values from the randomized data as well as a correlation coefficient for the relationship between co-occurrence and trait differences. There were no differences in the results using these two distribution randomization methods, but the randomization procedure was significantly faster using EcoSim. For all of the null models, 1,000 simulation matrices were generated to determine an underlying distribution against which to compare the observed results.

Co-occurrence and Niche Overlap at Different Phylogenetic Scales

Co-occurrence and niche overlap were calculated at different phylogenetic levels of resolution by comparing taxon pairs at all nodes on the basis of the phylogenetic relationships shown in figure 3. In the first set of analyses, we calculated co-occurrence and niche overlaps of sister species and then cumulated abundances of taxa in successively larger clades at higher phylogenetic levels, adapting methods described by Silvertown et al. (2001). Co-occurrence and niche overlap were computed for taxon pairs at each node. The highest level was a test between the red oak clade and the white + live oak clade. Relative basal area data was used as the raw data matrix, and values for higher taxa were calculated by summing the relative basal area of each species in the clade within each plot and dividing by the number of species in the clade. Niche overlap or co-occurrence of these taxa was then calculated as previously described. In the second set of analyses, co-occurrence and niche overlap were computed for all pairwise combinations of species within increasingly inclusive clades. Species pairwise co-occurrence and niche overlap values were then averaged for each clade and compared with null model 2. This second test allowed us to isolate the clades within which species showed evidence for lower than expected co-occurrence at the plot level or niche partitioning along a soil moisture gradient.

Convergence and Conservatism of Traits and Habitat Preferences

The convergence or conservatism of traits can be tested by correlations between trait differences and phylogenetic distance between species (Legendre et al. 1994; Böhning-Gaese and Oberrath 1999; Cavender-Bares and Wilczek 2003); for related methods, see Ackerly and Donoghue (1998), Burt (2001), and Blomberg and Garland (2002). We correlated pairwise trait differences with phylogenetic distances and compared the correlation coefficient to the distribution of correlation coefficients from a null model generated by randomizing the species across the phylogeny 1,000 times in order to shuffle the phylogenetic distance scores (null model 1). Using a two-tailed test, we find that a positive correlation, relative to the null model, indicates trait conservatism; a negative correlation indicates trait convergence. Because convergent traits will be dissimilar in both closely related pairs and some distantly related pairs, the magnitude of negative correlations is constrained, and the null model is essential to evaluate significance. In general, it should be noted that the accuracy of measures of conservatism depends on the completeness

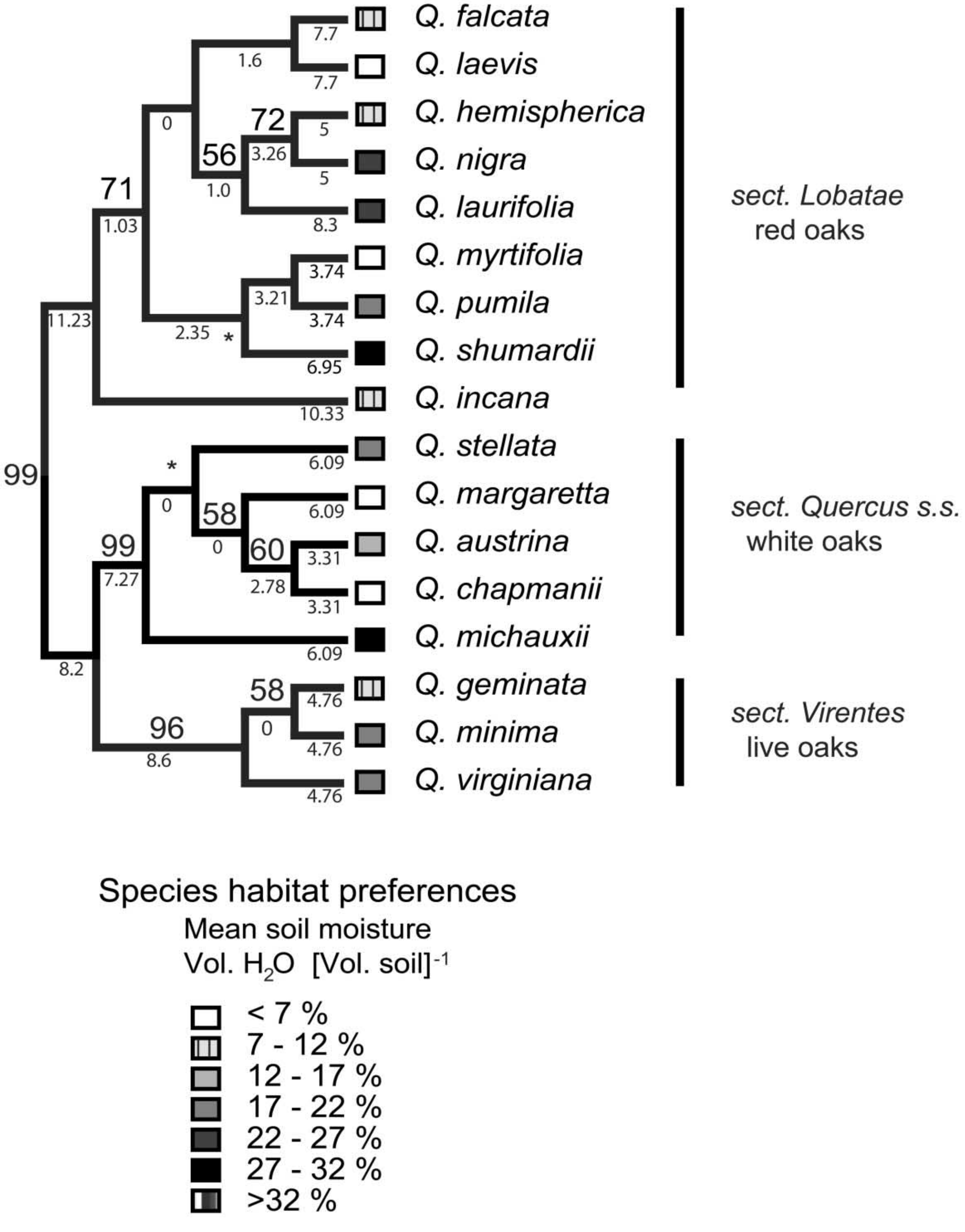


Figure 3: Phylogenetic relationships of 17 species of sympatric oaks in northern central Florida (one of four most parsimonious trees). Bootstrap values above 50% are given above branches, and branch lengths (HKY + clock) are given below branches. Asterisks indicate the branches that are not in agreement among the four tree topologies. Mean soil moisture values of species' habitat preferences are indicated by shaded boxes representing seven soil moisture bins. Dark shades indicate wet habitats, while light shades indicate dry habitats. Within both the red oak and white + live oak clades, species occupy wet, dry, and mesic habitats. None of the species have mean soil moisture preferences in the wettest soil moisture bin.

of the phylogeny, since missing taxa could cause biases (Webb et al. 2002).

A similar analysis was done to test for habitat convergence. On the basis of a priori observations that oaks from different taxonomic groups often show convergence in their habitats (Whittaker 1969; Cody and Mooney 1978; Mohler 1990; Jackson et al. 1999), we used a one-tailed test to determine whether habitat preferences of oak species showed a more negative correlation with phylogenetic distance (indicating convergence) than expected.

Phenotypic Clustering and Overdispersion

Traits important for environmental filtering are likely to be similar among co-occurring species and species with high niche overlaps (Webb et al. 2002). Pairwise trait differences between species were correlated with pairwise co-occurrence and niche overlap scores to determine whether there was evidence for phenotypic clustering or overdispersion. Phenotypic clustering would be indicated by a trait for which there was a significant negative correlation between the pairwise trait differences and co-occurrence or niche overlap (i.e., co-occurring species have a high degree of phenotypic similarity; Cavender-Bares and Wilczek 2003). Phenotypic overdispersion would be indicated by a positive correlation between trait differences and co-occurrence or niche overlap. Traits that show significant overdispersion within communities may contribute to competitive exclusion among species with similar trait values. Significance levels were determined by comparing the observed correlation coefficients for trait differences versus co-occurrence or versus niche overlap to the distribution of correlation coefficients generated using null model 1.

Results

Phylogenetic Analysis

Four most parsimonious trees were found (fig. 3). These topologies are consistent with previously published phylogenies of oaks (see fig. A2 in the online edition of the *American Naturalist*; Manos et al. 1999, 2001; Manos and Stanford 2001). Analysis of multiple accessions from individual species (not shown) showed little evidence of reticulation among distantly related species in these Florida communities, in contrast to previous studies of oaks (Whittemore and Schaal 1991; Dumolin-Lapegue et al. 1999) but consistent with a recent study of European oaks (Muir et al. 2000). Our results are consistent with the hypothesis that interspecific gene flow is reduced in Florida, where the growing season is long enough for species to flower at different times (Nixon et al. 1997).

Habitat Convergence

We found that Floridian oak species show a tendency toward evolutionary convergence in habitat preferences, illustrated by the negative relationship (relative to the expected r value) between critical habitat features, including soil fertility and fire regime, and phylogenetic distance. In particular, there was a significant negative correlation between species differences in soil moisture preference and phylogenetic distance (table 1). Thus, distantly related species share more similar soil moisture preferences, and closely related species share more contrasting preferences than expected by chance. This can be visualized by the color coding of mean soil moisture values of species habitats on the phylogeny in figure 3. Closely related species often show contrasting soil moisture preferences, and both red and white + live oak clades include species from xeric, mesic, and hydric habitats.

Phylogenetic Structure of Communities and Species Distributions across a Soil Moisture Gradient

Co-occurrence and Niche Overlap versus Phylogenetic Distance. We found that co-occurrence, calculated from basal area of oaks within plots, was more positively correlated with phylogenetic distance than expected (fig. 4; $P = .026–.047$; null model 1). This result was robust to tree topology (table 2) and branch length calculation method (not shown). The relationship was also significant if the basal area matrix was randomized (null model 2; not shown) rather than the phylogeny. This positive relationship indicates that closely related species seldom co-occur, whereas phylogenetically distant species have a higher probability of co-occurring. Such a pattern is evidence for phylogenetic overdispersion of closely related oak species. The same result was marginally significant ($P = .07–.088$) if co-occurrence was calculated from presence/absence

Table 1: Test of habitat convergence

	r	r exp	Obs < sim	P
Exchangeable phosphorus	−.005	.003	479	.521
Fire regime	−.045	.003	628	.372
Calcium content	−.036	.001	636	.364
pH	−.034	.003	659	.341
Exchangeable $NH_4 + NO_3$	−.067	.001	885	.115
Organic matter content	−.080**	.005	924	.076**
Soil moisture	−.092*	.009	982	.018*

Note: Correlation coefficients are shown for the relationship between differences in habitat preferences among species pairs and the phylogenetic distances between them. Soil moisture regime has a significantly more negative correlation than expected on the basis of a null model (one-tailed test) indicating habitat convergence.

* r values significant at $P < .05$.

** Marginally significant.

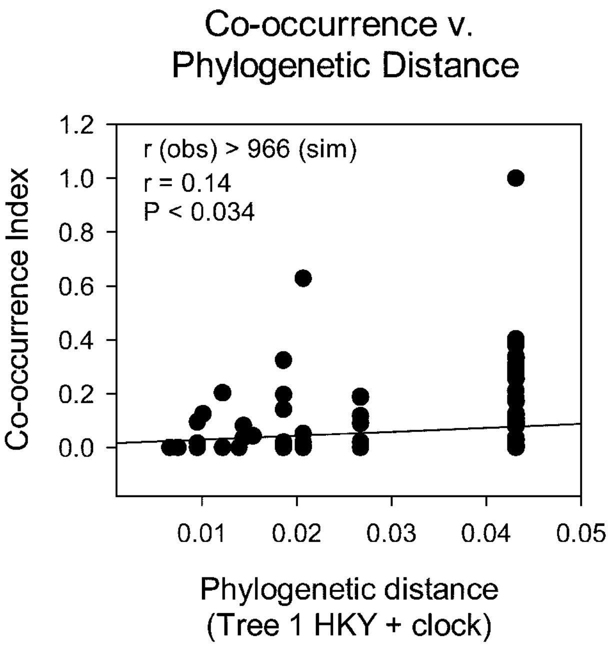


Figure 4: Species pairs with the least genetic distance between them show the lowest degree of co-occurrence resulting in a significant positive correlation between the co-occurrence index, calculated from basal area of oak trees within plots, and phylogenetic distance when compared with a null model in which species are randomized on the phylogeny. Phylogenetic distance is calculated using the HKY + clock model of evolution. Results of randomization tests for both co-occurrence and niche overlap based on basal area matrices are shown in table 2 and are based on presence/absence data matrices in table A1 in the online edition of the *American Naturalist.*

rather than from basal area. The higher significance levels of these tests using basal area rather than presence/absence are likely to result from the higher resolution achieved by using basal area. We ran the same test correlating pairwise niche overlap values with phylogenetic distance, and the results showed the same pattern of phylogenetic overdispersion. Niche overlap was more positively correlated with phylogenetic distance than expected ($P = .01$–$.036$; table 2).

Co-occurrence and Niche Overlap at Different Phylogenetic Scales. Table 3 shows the patterns of co-occurrence and niche overlap between clades at different levels of phylogenetic resolution and between species pairs within clades at different levels of resolution. We found that species co-occurred less often than expected within the white oak and the white + live oak clades (bottom of table 3). Within the red oak clade, there was a similar trend, but there is some degree of overlap among red oaks species. Co-occurrence is significantly less than expected within the red oaks when mean species co-occurrence is calculated for the clade one node shallower (which excludes *Quercus incana*; bottom of table 3, node 4). Within the live oaks, co-occurrence was not less than expected. The highest degree of overdispersion occurs at the intermediate phylogenetic scale, that is, at the second or third node (table 3). In contrast, at the deepest node, we find that the red oak group and the white + live oak groups show a higher degree of co-occurrence than expected by chance (table 3). The pattern is highly significant whether calculated from basal area ($P = .004$) or presence/absence ($P = .008$; not shown). This result indicates that at small spatial scales in any given patch (0.10-ha plot), there is a high likelihood that members of both the red and white + live oak group will be present.

The same analyses were carried out to investigate at what level of phylogenetic resolution species exhibited greater or less niche overlap than expected. In general, these results are similar to those described for co-occurrence. Species within the red oak clade and within the white + live oak clade showed significantly less niche overlap than expected by chance, indicating that radiation into all soil moisture niches has occurred in both clades. These results can be visualized for distributions of white + live oak species (fig. 5*A*) and red oak species (fig. 5*B*), respectively, across the soil moisture gradient. Within the white oak clade by itself, species showed significantly less overlap than expected (table 3). In contrast, among the live oaks, species did not show less overlap than expected. When the analysis was done at different phylogenetic levels by cumulating the abundances of taxa within clades, overlap at the deepest phylogenetic node showed that the red oak group overlaps with the white + live oak group significantly more than expected by chance ($P = .022$).

Combined, these results indicate that niche partitioning is occurring among taxa at the most highly resolved scale, that is, at the species level, so that closely related species occur in contrasting habitats. However, the highest degree of niche partitioning between lineages is actually occurring at intermediate phylogenetic scales at a depth of two and three nodes. At the deepest phylogenetic split, there is more overlap than expected between the two major clades because niche radiation into all possible soil moisture environments has occurred within both of them (table 3). Distributions of taxa across the soil moisture gradient within the white + live oak lineage (fig. 5*A*) resemble the distributions of taxa within the red oak lineage (fig. 5*B*). When the relative basal area of members of each of the two major clades are cumulated within each soil moisture level and normalized by the number of plots within each soil moisture level, the distributions of the red oaks and the white + live oaks show very similar and highly overlapping patterns (fig. 5*C*).

Table 2: Test of phylogenetic overdispersion

	Co-occurrence				Niche overlap			
Tree	r	r exp	Obs < sim	P	r	r exp	Obs < sim	P
1	.140*	−.001	965	.035*	.118*	−.002	973	.027*
2	.140*	.007	960	.040*	.111*	−.001	990	.010*
3	.136*	.000	953	.047*	.118*	−.002	964	.036*
4	.138*	−.007	974	.026*	.116*	−.004	974	.026*

Note: Correlation coefficients are given for the degree of co-occurrence or niche overlap (calculated from basal area of oak species within plots) versus phylogenetic distances between species. Correlations were calculated for four tree topologies using HKY + clock branch lengths. Observed values were compared with a null model with 1,000 randomizations. The correlations were more positive than expected (one-tailed test) indicating phylogenetic overdispersion.

* r values significant at $P < .05$.

Convergence and Conservatism in Functional Traits

Randomization tests for the relationship between trait divergence and phylogenetic distance revealed the degree to which functional traits were conserved or convergent (table A1 in the online edition of the *American Naturalist*; fig. 6). Acorn maturation time, vulnerability to freezing, wood density, and average vessel diameters were significantly conserved. Leaf life span and specific leaf area also showed a tendency toward conservatism. While many traits showed a lack of conservatism, no traits were more convergent than expected on the basis of a random distribution of traits across the phylogeny. Some degree of evolutionary convergence is indicated by a correlation coefficient that is negative relative to the expected r value, including traits related to fire regime and growth—such as rhizome resprouting potential, asymptotic height, and shoot transpiration—as well as seedling absolute growth rate and seedling canopy transpiration (table A1; fig. 6).

Ecological Filtering

Independent contrasts provide strong evidence for correlated evolution of functional traits and habitat preferences (all correlations discussed here are based on independent contrasts using the ITS phylogeny; table A2 in the online edition of the *American Naturalist*). For example, whole shoot transpiration of mature trees normalized by sapwood area, measured across the range of their distributions in the field, and seedling canopy transpiration rates, measured under common conditions in a glasshouse, were positively correlated with soil moisture preferences. Maximum hydraulic conductance of mature trees, percent loss of conductivity, vessel diameters, and seedling growth rate were also correlated with soil moisture preferences (table A2). Radial growth rates of mature trees and seedling growth rates in the common garden were positively correlated with species soil fertility preferences (e.g., for exchangeable nitrate + ammonium), as were asymptotic height and other traits correlated with soil moisture, such as percent loss of conductivity, whole shoot transpiration of mature trees, and seedling canopy transpiration rates (table A2).

With respect to fire regime, the outer bark thickness of saplings was negatively correlated with the fire return interval index, indicating that species experiencing more frequent fires have thicker bark (table A2). Note that this analysis excludes scrub species, which have thin bark and experience severe and relatively frequent fires in which bark offers little protection. Instead, these species are short in stature and have a high rhizome resprouting potential. A clear trade-off exists between rhizome resprouting potential and asymptotic height ($r = -0.84$, $P = .0004$). Several traits were negatively correlated with fire severity ranking, including asymptotic height, radial growth rate, and seedling growth rates. Rhizome resprouting potential was positively correlated with the fire severity index (table A2). While a number of traits were strongly correlated with habitat preferences, other traits, such as leaf life span and acorn maturation time, showed no correlation with soil moisture, soil fertility, or fire regime (table A2).

Phenotypic Clustering and Overdispersion

Several traits, including bark thickness, radial growth rate, seedling absolute growth rate, and rhizome resprouting potential, showed higher phenotypic clustering than expected, indicating that co-occurring species or species sharing the same niches across a soil moisture gradient were phenotypically similar. This was determined by a more negative correlation coefficient for trait divergences versus co-occurrence or niche overlap than expected (table A3 in the online edition of the *American Naturalist*; fig. 6). Several other traits showed trends toward phenotypic clustering, including whole shoot transpiration, seedling whole canopy transpiration, seedling absolute growth rate, and maximum hydraulic conductance. These traits are

Table 3: Co-occurrence and niche overlap at different phylogenetic levels

Phylogenetic depth and major clade	Taxa	Co-occurrence			Niche overlap			
		Obs < sim	*P*	+/−	Obs < sim	*P*	+/−	*N*
Between clades:								
6 nodes:								
R/WL	Red oaks vs. white + live oaks	2	.004*	+	11	.022*	+	
5 nodes:								
R	FA + LV + HE + NI + LA + MY + PM + SH vs. IN	24	.048*	+	562	.876		
W/L	White s.s. vs. live	912	.176		823	.354		
4 nodes:								
R	FA + LV + HE + NI + LA vs. MY + PM + SH	649	.702		755	.49		
W	ST + MA + AU + CH vs. MX	603	.794		192	.384		
3 nodes:								
R	FA + LV vs. HE + NI + LA	1,000	<.001*	−	1,000	<.001*	−	
W	MA + AU + CH vs. ST	993	.014*	−	994	.012*	−	
2 nodes:								
R	HE + NI vs. LA	752	.496		494	.988		
R	MY + PM vs. SH	600	.4		1,000	<.001*	−	
W	AU + CH vs. MA	988	.024*	−	898	.204		
L	GE + MN vs. VI	783	.434		691	.618		
1 node:								
R	FA vs. LV	773	.454		200	.4		
R	HE vs. NI	952**	.096**	−	979	.042*	−	
R	PM vs. MY	291	.709		852	.148		
W	AU vs. CH	556	.888		648	.704		
L	GE vs. MN	248	.496		781	.438		
L	GE vs. VI	526	.948		934	.132		
L	VI vs. MN	605	.79		461	.922		
Species within clades:								
5 nodes:								
R	Red oaks	914	.172		1,000	<.001*	−	9
WL	White + live oaks	1,000	<.001*	−	1,000	<.001*	−	8
4 nodes:								
R	FA, LV, HE, NI, LA, MY, PM, SH	1,000	<.001*	−	1,000	<.001*	−	8
W	White oaks s.s.	992	.016*	−	1,000	<.001*	−	5
3 nodes:								
R	FA, LV, HE, NI, LA	1,000	<.001*	−	1,000	<.001*	−	5
W	ST, MA, AU, CH	1,000	<.001*	−	998	.004*	−	4
2 nodes:								
R	HE, NI, LA	971	.058**	−	931	.138		3
R	MY, PM, SH	792	.416		1,000	<.001*	−	3
W	MA, AU, CH	993	.014*	−	960	.08**	−	3
L	Live oaks	670	.66		922	.156		3

Note: In the top half, clades were compared at phylogenetic nodes of increasing depth (deepest node shown first). Number of simulations out of 1,000 in which observed values were less than or equal to expected is shown. Tests showing a higher degree of co-occurrence or niche partitioning than expected (two-tailed) are indicated by a plus sign, and those showing less co-occurrence or niche overlap than expected are indicated by a minus sign. For higher taxa, relative basal area of each member species was summed to determine the distribution for the whole clade. In the bottom half, results of tests for means of pairwise co-occurrence and niche overlap values for all possible species pairs within decreasingly inclusive clades are shown. A minus sign indicates that species showed lower co-occurrence or niche overlap with each other than expected. *N* is the number of species within the clade. Major clade designations are shown to the left of the taxa included in each test: R = red oaks, W = white oaks, L = live oaks. Taxon codes: red oaks: FA, *Quercus falcata*; LV, *Q. laevis*; HE, Q. hemispherica; NI, *Q. nigra*; LA, *Q. laurifolia*; MY, *Q. myrtifolia*; PM, *Q. pumila*; SH, *Q. shumardii*; IN, *Q. incana*; white oaks: AU, *Q. austrina*; CH, *Q. chapmanii*; MA, *Q. margaretta*; MX, *Q. michauxii*; ST, *Q. stellata*; live oaks: MN, *Q. minima*; VI, *Q. virginiana*, GE, *Q. geminata*.

* $P < .05$.

** Marginally significant.

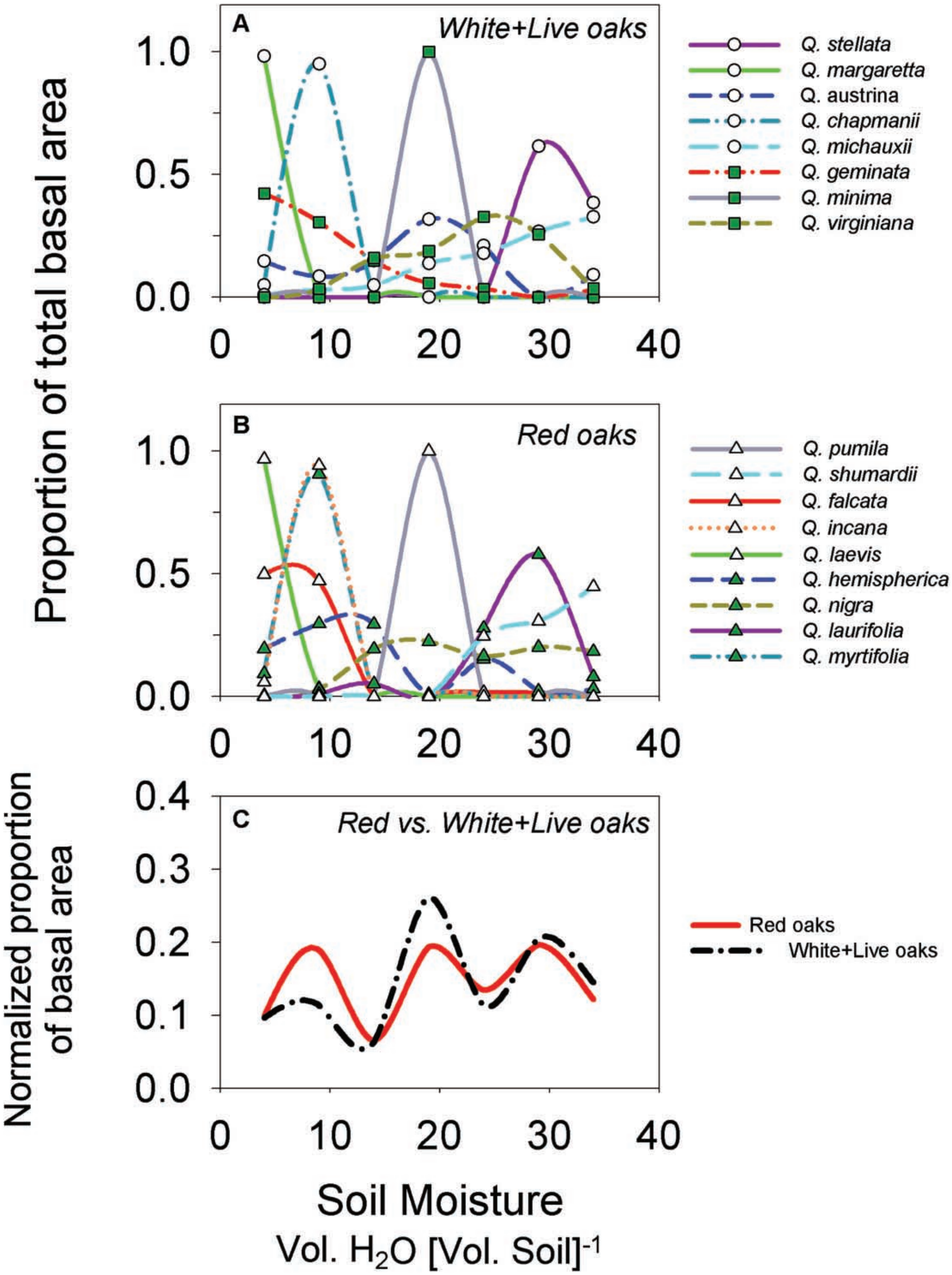


Figure 5: Proportion of total basal area across seven levels of soil moisture for the eight species in the white and live oak clades (*circles*, white oaks; *squares*, live oaks; *A*) and for the nine species in the red oak clade (*B*). Evergreen species are identified with filled symbols, and deciduous species are identified with open symbols. The collective distributions of the red oak clade and the white oak clade are shown in *C*. In *C*, the relative basal area of each species within a clade was summed within plots and within soil moisture levels and normalized by the number of plots within resource levels.

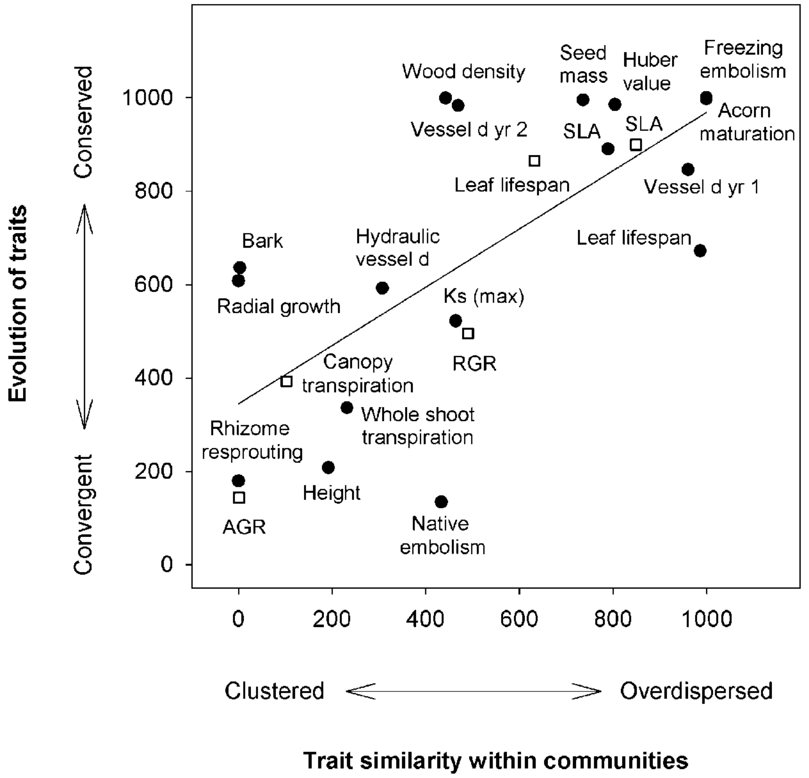


Figure 6: Conservatism of trait evolution in relation to the similarity of traits within communities. The *X*-axis indicates the number of simulations from the null model that are less than the observed value for the correlation of species pairwise trait differences with degree of co-occurrence. The *Y*-axis indicates the number of simulations from the null model that are greater than the observed value for the correlation of species pairwise trait differences with their phylogenetic distances. Axes are ordered with these orientations for comparison with figure 2. More convergent traits tend to be spatially clustered, and conserved traits tend to be overdispersed ($r = 0.71$). Filled symbols represent traits measured on mature trees; open symbols represent traits measured on seedlings in a common garden.

closely linked to fire regime, soil moisture, and fertility, as shown in table A2, and are likely to be important in the environmental sorting of species. Other traits, including acorn maturation time, embolism due to freezing, leaf life span, and first-year vessel diameters, show higher phenotypic dispersion than expected, as indicated by a significant or marginally significant positive correlation of trait differences versus co-occurrence (fig. 6) or niche overlap (table A3). Of these traits, several are either significantly or relatively conserved, including acorn maturation time, vulnerability to freezing, first-year vessel diameter, and leaf life span. Overall, there was a highly significant correlation between the conservatism of traits and their degree of overdispersion within communities ($r = 0.71$, $P < .01$; fig. 6). The same relationship is found when overdispersion is calculated from niche overlap rather than from co-occurrence ($r = 0.83$, $P < .01$). The potential significance of conserved traits in terms of species coexistence is addressed below.

Discussion

We have demonstrated significant convergence in the habitats of species (table 1) and lower co-occurrence among closely related congeners than expected (table 2). Within both of the major lineages (red oaks and white + live oaks), species show significant niche partitioning along a soil moisture gradient (fig. 5), such that closely related species show less niche overlap than expected and distantly related species show greater overlap than expected (table 2). These patterns of phylogenetic overdispersion in the assembly of oak-dominated communities result, in part, from convergent evolution in traits important for tolerating the abiotic environment (fig. 6). We also propose that conserved traits, those related to life history, are important in reducing competition among and promoting the coexistence of distantly related species. These mechanisms of coexistence provide an explanation for how oak diversity is maintained within local communities.

Environmental Filtering

Independent contrast correlations show strong evidence for correlated evolution of critical functional traits with habitat factors. For example, whole shoot transpiration, maximum hydraulic conductance, seedling absolute growth rate, and seedling canopy transpiration rates are positively correlated with species soil moisture and soil fertility preferences (table A3). Similarly, bark thickness of juveniles, rhizome sprouting potential, and asymptotic height are species traits that correlate with the prevailing fire regime in the three community types. In hammocks and sandhills, rapid growth and height extension offer an advantage in terms of competitiveness (access to light) or in terms of avoiding crown damage from ground fires. Species that invest in fast growth and tall stature would be expected to invest less in mechanisms that allow them to recover after severe fire. In contrast, species that experience severe fire regimes would be expected to invest less in aboveground biomass and stature and more in mechanisms of rapid recovery after fire. Within habitats, co-occurring species show similarities in traits (phenotypic clustering) that are likely to be critical to their survival in the abiotic environment (table A3; fig. 6), providing evidence for the environmental filtering hypothesis.

The Case for Phylogenetic Overdispersion

In contrast to other systems (e.g., Webb 2000), environmental filtering in oak communities does not lead to clustering of closely related species. Three separate analyses demonstrate a pattern of phylogenetic overdispersion among congeneric oak species in this landscape. First, distantly related oak species show convergence in critical habitat features when tested against null models (table 1). In particular, soil moisture preferences of species are significantly more convergent than expected (fig. 3; table 1). Second, the most closely related species have very low degrees of co-occurrence and niche overlap, resulting in a more positive than expected correlation between either the degree of co-occurrence of species pairs or their niche overlap and the phylogenetic distance between them (fig. 4; table 2). Finally, within both of the major lineages represented in Florida (red oaks and white + live oaks), niche breadths of individual oak species show less overlap than expected by chance. This latter pattern is most significant within the white oak clade (table 3). The highest degree of niche partitioning between lineages is occurring at intermediate phylogenetic scales at a depth of two and three nodes because some of the most recently diverged species pairs do not partition the soil moisture gradient more than expected if their distributions were random (e.g., *Quercus falcata* and *Q. laevis* or *Q. geminata* and *Q. minima*). At the deepest node between red oaks and the white + live oaks, the cumulative distributions of species within these two clades show greater co-occurrence and more overlap than expected (fig. 5). This pattern arises because species within each of these two major clades have expanded into all soil moisture regimes. These results clearly show that within the oak genus, closely related species are less likely to occur together or in similar soil moisture environments than expected. Furthermore, in any given community, species are likely to be drawn from both the red and white + live oak clade. This pattern has been previously observed in other oak communities (Mohler 1990) but never tested using phylogenetic methods.

Convergence of Traits Linked to Environmental Filtering

We explain the phylogenetic overdispersion in the assembly of Floridian oak communities first by the evolutionary lability of ecologically important physiological and morphological traits. Traits that correlate closely with habitat factors, such as soil moisture and fire regime, and hence are important for environmental filtering tend to be relatively convergent. Patterson and Givnish (2002) showed a similar pattern of convergence in multiple traits among core Liliales species in different lineages that share the same set of ecological conditions. In this study, seedling absolute growth rate, seedling canopy transpiration, mature tree asymptotic height, rhizome resprouting potential, and whole shoot transpiration show evidence of evolutionary convergence (table A1; fig. 6), and all of these traits are significantly correlated with critical habitat features using phylogenetically independent contrasts (table A2). Oak species that are phenotypically similar with respect to convergent traits also show higher co-occurrence (or niche overlap) than expected, as indicated by a negative correlation between trait divergence and co-occurrence (or niche overlap; table A3). One caveat that must be addressed is that traits measured on individuals in the field may tend to appear clustered among species that have a high degree of co-occurrence because of plastic responses to a common environment rather than because of heritable components of traits. However, traits measured on seedlings in a common environment, where plasticity is not a confounding factor, show the same correlation between trait evolution and trait similarity (fig. 6, *open symbols*). These observations suggest the generality that the long-term success of the oaks, which often co-occur with other oak species, has depended on having sufficient evolutionary potential to be able to move fluidly, in evolutionary time, along the gradient of ecophysiologically relevant environmental variation.

Conserved Traits and Species Coexistence

At the same time that convergent traits tend to show phenotypic clustering within communities and are adaptively linked to species abiotic environments (table A2), conserved traits show phenotypic overdispersion and are not correlated with measured abiotic factors. This gives rise to a strong correlation between trait evolution and trait similarity within communities (fig. 6) that explains the pattern of phylogenetic overdispersion, as predicted in figure 2. This result supports the hypothesis that both environmental filtering and species interactions have been important forces in structuring these communities.

The conserved, overdispersed traits are candidates for mechanisms likely to promote coexistence between distantly related species. For example, acorn maturation time may prevent closely related species from co-occurring and may reduce competition between species of different sections of the genus through mechanisms of complementarity, including asynchrony in masting and seedling regeneration. Acorn maturation time is highly conserved at the lineage level, 1 yr in white and live oaks and 2 yr in red oaks (with rare exceptions, e.g., *Q. pumila*; Nixon et al. 1997), and it does not seem important in environmental filtering as suggested by a lack of correlation with habitat variables (table A2). If a hard frost killed all the oak flowers in a given year, no white oaks would germinate that year, but red oaks could from the previous year's flowers. In contrast, the following year, recruitment of white oaks but not red oaks would be likely. This sets up the possibility that climatic variability could lead to staggering in the timing of regeneration among the two clades. Mohler (1990) used yearly acorn productivity data in diverse stands to show that there is higher asynchrony in masting among species pairs from different sections of the genus than expected. In communities where suitable patches for seedling regeneration are limiting, this phenomenon could reduce competition and increase the likelihood of co-occurrence between red and white oaks via temporal segregation in regeneration (Chesson and Warner 1981; Chesson 1985). Similarly, conservatism in seed predator-host relationships could lead to differences in dispersal patterns linked to phylogeny that could promote coexistence of distantly related species through lottery mechanisms (Chesson and Warner 1981). Conservation of secondary chemistry and lipid content of acorns among red and white oaks (Fowells 1965; Ofcarcik and Burns 1971; Short and Epps 1976; Smallwood et al. 2001) are likely mechanisms for lineage-level specificity among seed predators (Smallwood et al. 2001).

Host specificity of pathogens or herbivores within lineages could result in density-dependent interactions that would limit the co-occurrence of closely related species and promote the co-occurrence of distantly related species. There is evidence that red oaks are more susceptible to oak wilt (*Ceratocystis fagacearum)* than white oaks (Farr et al. 1989; Bruhn et al. 1991), which could potentially be linked to conserved differences in wood anatomy (e.g., vessel diameters and wood density; fig. 6). If pathogens tend to show conservatism in host specificity, two co-occurring red oak species are more likely to be influenced by the same density-dependent processes than are a pair of co-occurring red and white oak species. Empirical observation, combined with modeling approaches and experimental manipulations, could be used to test such hypotheses.

Leaf life span, a relatively conserved trait, shows significant phenotypic overdispersion such that co-occurring oaks are likely to have more contrasting phenologies than expected (table A3). This pattern is visually apparent in figure 5: species within the same clade that have overlapping distributions tend to have contrasting leaf habits (*filled symbols*, evergreen; *open symbols*, deciduous). Species with shorter-lived leaves are likely to have low nutrient use efficiency and to acquire resources in large quantities in the spring during their initial flushing period. Species with longer leaf longevities generally have lower peak resource uptake rates but acquire resources over a much larger proportion of the year, resulting in higher nutrient use efficiency (Kikuzawa 1991; Reich et al. 1992). Such contrasting mechanisms of nutrient use and timing of resource use may reduce competition between and increase compatibility of species with differing leaf longevities (Sakai 1992). Leaf longevity and phenology are highly conserved within the white oaks in this region (deciduous) and within the live oaks (evergreen) and may increase the likelihood of coexistence among white and live oaks. Within the red oak clade, however, they have somewhat lower fidelity to phylogenetic relationships. This may provide complementarity among some red oak species (see fig. 5) and could contribute to the less significant overdispersion in the red oak group relative to the white + live oak group (table 3). For example, *Q. falcata* (deciduous) and *Q. hemispherica* (evergreen) are two red oaks that have similar distributions and occur together fairly frequently (fig. 5). This example underscores the fact that the phylogenetic structure of community assemblages depends on the phenotypes of species. Only to the extent that phenotypic traits both reflect phylogenetic patterns and influence community assembly is phylogenetic structure expressed at the community level.

Niche Differentiation and Historical Species Interactions

The high convergence in habitat preferences we have demonstrated presents the intriguing possibility of parallel adaptive radiation into contrasting niches within both the red and white + live oak clades. The pattern is even more striking when we consider that soil moisture is only one niche axis. For example, *Q. myrtifolia* and *Q. laevis*, both red oaks, show completely overlapping distributions across the soil moisture gradient (fig. 5) but never occur together because of the fact that *Q. laevis* is tolerant of very frequent low severity fires, whereas *Q. myrtifolia* is adapted to severe, less frequent fires. In closed systems, such as islands where all descendants of a common ancestor occur in sympatry (Losos et al. 1998), the patterns of niche differentiation we show here (figs. 3, 5) would likely reflect character displacement and adaptive radiation driven by competition for scarce resources (Armbruster 1985; Schluter and McPhail 1992; Schluter 1996; Radtkey et al. 1997; Adams and Rohlf 2000; Price et al. 2000). Species with completely overlapping geographic ranges that are believed to be true sister taxa, such as species within the live oaks in this system, are good candidates for inferring evolved niche differentiation due to long-term competitive interactions. *Quercus virginiana* and *Q. geminata*, the two most common live oaks, show significant differences in growth rate in a common garden ($df = 17$, $P < .0028$) and show some evidence of niche divergence across a soil moisture gradient (fig. 5), although the trend is not significant (table 3). The clade including *Q. nigra*, *Q. hemispherica*, and *Q. laurifolia* (fig. 3) is also likely to be comprised of sister taxa (K. Nixon, personal communication), and there is a trend that these species co-occur less than expected ($P = .058$; table 3). In particular, *Q. hemispherica* and *Q. nigra* show significant differences in growth rate in a common garden ($df = 15$, $P < .02$) as well as significant niche partitioning across the soil moisture gradient ($P = .042$; table 3). Finally, *Q. stellata* (post oak) and *Q. margaretta* (sand post oak) are commonly considered to be each other's closest relative, and their current distributions show no overlap across a soil moisture gradient (fig. 5; $P < .001$). These examples, taken together, suggest that past competitive interactions among close relatives are likely to have caused some of the observed niche differentiation.

For the majority of species that co-occur in this region, however, inferences about the role of past competitive interactions in causing niche differentiation among currently sympatric species cannot be made. In this system, there is a large number of intervening taxa in the phylogeny that are not components of the ecosystem, and most of the species currently interacting in this region also co-occur with other species at other latitudes. Hence, the general pattern of niche differentiation by close relatives, observed in both of the major clades (table 3; fig. 5*A*, 5*B*), is unlikely to have resulted solely or even primarily from evolutionary divergence caused by past competitive interactions among the current assemblage of species. Both niche differentiation and the patterns of co-occurrence of multiple oaks at small spatial scales can be explained by habitat tracking and lineage sorting by species as a result of previously acquired traits (cf. Ackerly 2003): as new species arrived in this region in Florida, certain traits that confer environmental tolerances caused them to assemble along environmental gradients where they could persist, while other traits promoted coexistence among some species combinations but not others.

What then, if anything, can be inferred about the role of species interactions in influencing trait evolution in this system? Losos et al. (2003) argued that phylogenetic overdispersion is likely to occur among sympatric species that have a long history of competitive interactions causing evolutionary divergence to overcome the forces of niche conservatism that prevail when species have evolved in allopatry. Phylogenetic overdispersion among the oaks may thus be difficult to explain without invoking long-term species interactions. Indeed, Whittaker (1969) postulated a role for long-term species interactions in his hypothesis that the uncanny likelihood of red and white oaks to occur together must be the result of coevolved species pairs. Mohler (1990) later rejected this hypothesis by demonstrating a lack of consistency in the species identities of co-occurring red and white oaks across diverse stands.

Floristic treatments of the oaks of Central America (Muller 1942) add evidence to that presented by Mohler (1990) and the current study that the co-occurrence among red and white oaks is ubiquitous throughout the range of the genus in North America, including at the center of diversity (Mexico [Nixon 1993]). Furthermore, recent phylogenetic and biogeographical evidence (Manos et al. 1999; Manos and Stanford 2001) combined with fossil records (Daghlian and Crepet 1983; Tiffney and Manchester 2001) support earlier hypotheses (Axelrod 1983) that the major groups of oaks evolved near their current distributions. Hence, it is highly likely that throughout the radiation of the genus in the Americas, red and white oaks have always co-occurred, even though the species identities of co-occurring red and white oaks within any given community may have shifted. If competitive interactions are considered in terms of the likelihood of interactions among particular phenotypic traits rather than of particular species per se, a long history of competitive interactions among red oak species and white oak species could have provided a selective force contributing to the conservatism of traits distinct to each lineage that promote coexistence between them. For example, if the reversal to annual acorn maturation allowed the original white oak population to coexist with its red oak ancestor by causing asynchrony in masting and temporal segregation in regeneration, continued competition among subsequent generations, populations, and species of red and white oaks in different communities might have conserved this trait difference if, on balance, it increased the likelihood of survival of species in both lineages. Modeling approaches could be used to test the hypothesis that long-term competition between lineages could lead to evolutionary conservatism of traits that promote coexistence.

Conclusions

Our study shows that phylogenetic overdispersion is occurring among Floridian oaks and demonstrates that this phenomenon is dependent on the level of resolution of phylogenetic analysis. The dominance of these forests by oaks as a whole presumably reflects shared traits amenable to broadscale environmental conditions. Within the genus, however, co-occurring oak species are more distantly related than expected. This nonrandom phylogenetic pattern of community assembly arises because closely related species have radiated into different habitat niches. It may also be the result of greater ecological complementarity (minimizing competition) and reduced density-dependent mortality of more distantly related oaks. The diversity of oak species in a region ultimately depends on the rate of evolution of different traits. Traits that are most labile at the species level are those that are critical for lineages to switch between available habitats and community types. In contrast, traits that are more conserved and that characterize the major lineages are those that facilitate coexistence. This illustrates that the diversity and ecological dominance of clades such as the oaks may be related to the phylogenetic scale at which these different trait types evolve.

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