Phylogenetic repulsion in the assembly of Floridian oak communities

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Abstract

Plant species that occur together in communities and experience similar environmental conditions are likely to share phenotypic traits due to the process of environmental filtering. At the same time, species that are too similar are unlikely to co-occur due to competitive exclusion. Communities that are dominated by multiple species of a single genus are challenging to explain because they appear to present an exception to the principle of competitive exclusion. We examined the phylogenetic structure of oak dominated forest communities in north central Florida in relation to ecological and physiological traits of the seventeen species of oaks that occur in this region. Oak species co-occurring within communities are more distantly related than expected by chance, and the most closely related species occur in the same communities less often than expected, providing evidence for phylogenetic repulsion. Within individual clades, species tend to show spatial overdispersion among plots and greater niche partitioning across a soil moisture gradient than expected. However, cumulative distributions of species in the two major clades (i.e., red oaks and white+live oaks), representing the deepest phylogenetic node, show greater niche overlap than expected. Hence communities are more likely to include members of both the red oak and the white+live oak clades than expected by chance and the distributions of the two clades across a soil moisture gradient are significantly more similar than expected. This pattern of phylogenetic repulsion within clades can be explained because traits important for habitat specialization show high evolutionary convergence. At the same time, we hypothesize that certain conserved traits permit coexistence of distantly related congeners.

Introduction

A critical challenge in community ecology is to understand how the ecophysiological attributes of species influence community assembly and how these attributes, and hence community composition, change over evolutionary time scales. There are two central processes involved in the assembly of communities 1) the ecological filtering of species that can exist within a community based on the abiotic environment (Weiher and Keddy 1995; Weiher et al. 1998) and 2) limitations to long-term coexistence including competitive exclusion (Gause 1934; Elton 1946; MacArthur and Levins 1967; Chesson 1991; Leibold 1998). These two processes make opposite predictions about the phenotypic and phylogenetic similarity and dissimilarity of co-occurring species (Tofts and Silvertown 2000; Webb 2000). If closely related species share similar physiological limitations and exhibit evolutionary niche conservatism, the former process, ecological filtering, will tend to cause closely related species to co-occur; this pattern can be termed phylogenetic attraction or underdispersion.   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). On the other hand, competitive exclusion should limit the coexistence of closely related species that are phenotypically similar, leading to the opposite pattern of phylogenetic repulsion, with co-occurring species being phylogenetically overdispersed. This latter pattern has been hypothesized but has yet to be demonstrated using phylogenetic analysis.

Communities that are dominated by multiple species of a single genus are challenging to explain because they appear to present an exception to the principle of competitive exclusion. Most studies of this problem have focused on niche and character differentiation of sympatric congeneric species(Wilson and Lee 1994; Price et al. 2000), in an effort to find ecological and evolutionary mechanisms that may prevent competitive exclusion (Armbruster 1985; Schluter and McPhail 1992; Schluter 1996; Radtkey et al. 1997; Adams and Rohlf 2000). It is also important to look beyond the genus designation, and consider phylogenetic relationships at higher resolution. Phylogenetic repulsion or attraction may occur at any level of phylogenetic resolution (Silvertown et al. 2001),

reflecting patterns of trait evolution and the relative importance of ecological filtering and competitive exclusion (Webb et al. 2002).

Oak-dominated forests provide an important model system to address these questions in plant communities. In North Central Florida, seventeen species of oaks co-occur. The high diversity of congeneric species 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. submitted). However, at small spatial scales, up to six species of oaks can still occur within a single 0.10 ha plot. In this study, we investigated the phylogenetic structure of co-occurring oak species in these communities and examined the phenotypic traits and habitat features likely to give rise to this structure. We estimated the phylogeny of the co-occurring oaks using molecular data, and we used environmental, ecophysiological, and morphological measurements in the field and greenhouse (reported in Cavender-Bares and Holbrook 2001; Cavender-Bares et al. submitted) to identify key functional traits and habitat features. We set out to test the hypothesis that co-occurring congeneric species would show patterns of either phylogenetic repulsion (due to factors limiting coexistence of phenotypically similar species), or phylogenetic attraction (due to niche conservatism), or both patterns at different phylogenetic scales. In order to test this hypothesis we combined four different kinds of data sets and developed a series of metrics for examining the phylogenetic and phenotypic structure of community assemblages. Null models assuming random spatial distributions (with constraints) or randomized phylogenetic relationships between species were used to examine the departure of observed patterns from expected patterns. A conceptual overview of this approach is outlined in Figure 1.

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; Manos et al. 2001; Manos and Stanford 2001). For this study, it was necessary to estimate the phylogenetic relationships among the seventeen Floridian oak species occurring in our study system. We sequenced the internal transcribed spacers and 5.8S coding sequence of nuclear ribosomal DNA (ITS) and estimated the phylogeny using maximum parsimony and maximum likelihood.

Voucher specimens for the seventeen Florida oak species, including UTM coordinates for source tree locations, are held at the Harvard University Herbaria. Genomic DNA was isolated from fresh leaf material for each species and extracted using the DNeasy Plant Mini Kit (QUIAGEN Inc.; Valencia, California). The ITS region was amplified using PCR with flanking primers ITS.LEU and ITS.4, plus internal primers ITS.2 and ITS.3B (Baum et al. 1994). The cleaned, quantified product was sequenced using the ABI Prism Big Dye Terminator Cycle Sequencing Reaction Kit (PE Applied Biosystems; Foster City, California) and then run on an ABI Model 377 automated DNA sequencer using Long Ranger gels (FMC Bioproducts; Rockland, Maine). Contigs were assembled using Sequencher version 3.0 (Gene Codes Corp.; Ann Arbor, Michigan). The sequencing strategy allowed the entire region to be sequenced in both directions except for close to the priming sites. Sequences were obtained from three to five individuals per species, as a check for problems of hybridization or cryptic variation. For each species, the sequence with the fewest ambiguous nucleotides was used in the final data matrix or if there was no difference in sequence quality, one sequence was chosen at random.

The data matrix was created by combining the sequences from the 17 Florida species with 20 sequences of other oak species obtained from GenBank (Appendix 1). Sequences were easily aligned manually. 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 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 if there was an effect of the addition of

further taxa we also analyzed the complete 37 taxon matrix. 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 are incompatible with the strict consensus from the previous search.

Branch length estimation

Branch lengths were calculated on all four most-parsimonious trees using two different models of evolution using PAUP* 4.0b7 (Swofford, 2001): (1) 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). (2) HKYclock—As in 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 cannot be rejected and is therefore the preferred method of branchlength calculation. Based on this result, we use HKYclock branchlengths in all of the analyses.

Field sampling

Quantitative data on vegetation and soil variables were collected from randomly established 0.10 ha (20 x 50 m) plots in three state preserves in northern central Florida (see Cavender-Bares et al. submitted). The preserves included San Felasco Hammock State Preserve, a 2803 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. Random plots were established in each park for a total of 74 plots. Within each plot, the dbh of each oak tree over 1.3 m 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. A histogram showing the number of oak species per plot is shown in Fig. 1.

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 of at the University of Florida. Soil moisture to 1 m depth was repeatedly measured using time domain reflectometry in four suplots of each plot over a 14 month period during both wet and dry cycles, as described in Cavender-Bares and Holbrook (2001). Species habitat preferences for soil factors were determined from weighted mean values of soil moisture and soil fertility for species distributions across the three state preserves. A detailed description of the field methods are presented in Cavender-Bares et al. (submitted).

Measurement of traits

A suite of functional traits were 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 (Cavender-Bares and Holbrook 2001; Cavender-Bares et al. submitted). Traits examined include acorn maturation time (years), vulnerability to freezing (percent loss of hydraulic conductivity after freezing-induced xylem cavitation), average and maximum leaf lifespan (days), wood density (g cm^{-3}), vessel diameters of first and second year wood of sunlit branches (μm), sapling outer bark thickness (cm), asymptotic height (m), radial growth rate (mm yr^{-1}), rhizome resprouting potential (an index based on ability to spread clonally and resprout from underground rhizomes and roots), native embolism measured as percent loss of hydraulic conductivity, maximum hydraulic conductivity (kg H_2O m MPa s^{-1}), and whole shoot transpiration normalized by sapwood area (mmol H_2O m^{-2} s^{-1}). Traits measured on seedlings included relative growth rates (g g^{-1} day^{-1}), absolute growth rates (g yr^{-1}), whole canopy transpiration rates (mmol H_2O s^{-1} $plant^{-1}$).

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 (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 1997; Greenberg and Simons 1999) according to the following criteria: 1) no resprouting from rhizomes or roots 2) infrequent vegetative reproduction from rhizomes or roots 3) frequent vegetative reproduction from rhizomes and/or roots including clonal spreading and dome formation. Sapling outer bark thickness was measured adapting methods described by Jackson et al (1999) and (Adams and Jackson. 1995). Data for several species was taken from Jackson et al. (1999). Acorn maturation time, or number of years for the acorns to develop to maturity, was taken from Nixon (1997).

Measurement of all other leaf-level and whole plant traits examined in this study were carried out on 6 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 lifespan was calculated from leaf birth and death dates monitored on three branches per tree. We give two measures of leaf lifespan: maximum leaf lifespan is the lifespan of the first cohort of leaves; average leaf lifespan is the lifespan averaged across all leaf cohorts. Maximum leaf lifespan was very similar to average leaf lifespan but was less dependent on the timing of the onset of cold weather. Radial growth increment, a measure of absolute growth rate, was calculated from tree ring widths from tree cores of mature trees. We measured tree ring widths only for the last ten years of growth to ensure that measurements were made only for years when the canopies were exposed.

Seedling relative and absolute growth rates were measured on a subset of 9 species, including *Q. falcata, Q. geminata, Q. hemispherica, Q. laevis, Q. margaretta, Q. michauxii, Q. myrtifolia, Q. nigra, and Q. virginiana*, grown under optimal condition in a glasshouse at Harvard University. Absolute growth rate was determined by dry biomass after one year of growth. Relative growth rate was calculated as follows:

$$\text{RGR} = \frac{Log_e(M_{final}) - Log_e(M_{initial})}{T_{final} - T_{initial}} \qquad (1)$$

where M_{final} and $M_{initial}$ are biomass at the time of harvest (T_{final}) and the time of transplanting ($T_{initial}$) (Hunt 1982). Seedling whole plant transpiration rates were calculated by multiplying mean maximum transpiration rates per species by the average

leaf surface area per species. Detailed methods for leaf-level and whole plant traits are presented in Cavender-Bares and Holbrook (2001) and in Cavender-Bares et al. (submitted).

Multiple analysis of variance

One simple way of finding evidence for phylogenetic niche conservatism is to determine how much of the variance in species spatial distributions, habitat factors, and functional traits can be explained by clade membership (Harvey and Pagel 1991). We focused this analysis on the deepest and best supported splits in the oak phylogeny by dividing taxa into either two clades (red oaks and white+live oaks) or three clades (red oaks, white oaks and live oaks). Three separate MANOVAs were computed for 1) relative spatial relationships of species given by the first and second axis scores of oak species from detrended correspondence analysis of occurrences of all woody species within 74 random 0.10 ha plots (reported in Cavender-Bares et al. submitted), 2) Species habitat preferences for soil moisture, exchangeable phosphorus, calcium content, organic matter content, and exchangeable nitrate+ammonium, calculated as weighted means of species' distributions along these resource axes; and 3) functional traits, including sapling outer bark thickness, vessel diameter, leaf lifespan, specific leaf area (SLA), percent loss of hydraulic conductivity (PLC), wood density, radial growth rate, rhizome resprouting potential, asymptotic height, acorn maturation time, and whole shoot transpiration normalized by sapwood area. We then calculated three additional MANOVAs, with the same sets of dependent variables, but used community affiliations (sandhill, scrub and hammock) as the main fixed effects. Species affiliations 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. geminate, Q. pumila, Q. minima*. All analyses were done using Data Desk (Velleman 1995).

Phylogenetic structure of communities

Co-occurrence of species was determined by recording the basal area of 17 oak species in seventy-four randomly established 0.10 hectare plots in three state parks

(Cavender-Bares and Holbrook 2001). Pairwise values of co-occurrence were calculated using a co-occurrence index (CI) based on proportional similarity (cf., Schoener, T.W. 1970): $CI_{ih} = 1 - 0.5 * \Sigma |p_{ij} - p_{hj}|$, 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. We tested whether there was a significant correlation between the patristic distance of pairs of taxa and their degree of co-occurrence. The patristic distance is the sum of the estimated lengths of all intervening branches on the phylogeny. The correlation coefficient obtained was compared to two null models. For the first null model, species were randomized 1000 times across the phylogeny, causing a shuffling of the patristic distance scores (see Lapointe and Garland 2001). For the second null model, patristic distances were kept fixed, and 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. Distribution data were randomized using the knights tour algorithm (Gotelli and Entsminger 2001b) using a program written in Visual Basic (available upon request) or by the sequential swap method in the null model software, Ecosim (Gotelli and Entsminger 2001a). 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.

A similar test was done for niche overlap by correlating pairwise values of niche overlap with phylogenetic distance and comparing them to a null model. The niche structure of these 17 oak species was examined by using soil moisture as the primary niche axis. Soil moisture is a critical environmental gradient influencing plant species distribution in northern central Florida and is highly correlated with fire frequency (Ewel 1990, Jackson, 1999 #1213) and soil fertility (Cavender-Bares et al, submitted), two other important environmental factors in this region (Monk 1968; Myers and Ewel 1990) . Mean soil moisture levels over a 14 month period, including during extreme conditions, were calculated within each of the 74 0.10 ha plots. Niche overlap was computed for seven soil moisture levels, each spanning a change of approximately 4% soil moisture,

based on Pianka's species overlap index (Pianka 1973), using either presence/absence or
basal area as the raw data matrix according to the following equation:

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

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. Basal area was standardized so
that it summed to 1 for each taxon across all niche bins. Again, the null model was 1000
randomizations of species across the phylogeny to generate random pairwise patristic (or
phylogenetic) distances.

Co-occurrence and niche overlap at different phylogenetic scales

Co-occurrence and niche overlap were calculated at different phylogenetic scales
by comparing taxon pairs at all nodes based on the phylogenetic relationships. 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. When relative basal area data was used as the
raw data matrix, 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. When presence/absence data was used, the higher taxon was considered
present (given a score of one) if any member of the clade occurred in the plot. 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
to the null model.

We used two null models to accommodate the two types of raw data used in the calculations. For basal area, the null model was generated by randomizing basal area values across plots, constraining species totals, as above. For presence/absence data, row totals (plots) and column totals (species) were constrained. In all of these analyses, each randomization was run 1000 times and the observed overlaps were compared to the distribution of the overlap values calculated from the randomized data. The null model for the presence/absence data is most realistic biologically because it constrains the total occurrences of species as well as the total number of species per plot. However, presence/absence data does not provide the same degree of resolution for the distributions of species as basal area because differences in relative abundance within plots are not considered. The same null model could not be used for basal area values, however, as it would be quite difficult to achieve randomization and still constrain the total basal area per species.

Independent Contrast Correlations

One method for examining ecological 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) specifically allows examination of whether there is 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. Soil fertility is reported as exchangeable nitrate+ammonium (mg kg^{-1}); this measure is highly correlated with other soil fertility factors (Cavender-Bares et al. submitted). 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 (see below). 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 ecosystems that follow a gradient of fire severity and

correspond to the three community types previously discussed: (1) Low or unpredictable severity and very low frequency fires (100 to 1000 years) that occur in hammock areas of high soil moisture and rapid decomposition; (2) intermediate severity and high frequency fires (every 1 to 7 years) 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 (3) very high severity fires that occur with predictable frequency (on the order of every 50 years) but destroy the above ground biomass, facilitated by fire resistance of the vegetation in scrub communities until fuel build-up is high. Independent contrast calculations were done in the CACTUS computer program (Schwilk 1999) and were tested over four tree topologies and 6 branch length distributions.

Trait convergence and conservatism

The convergence or conservatism of traits can be revealed by correlations between trait divergence and phylogenetic distance between species (Legendre et al. 1994; Böhning-Gaese and Oberrath 1999; Cavender-Bares and Wilczek 2003); for related methods, see (e.g., Ackerly and Donoghue 1998; Burt 2001; Blomberg and Garland 2002). We correlated pairwise trait differences with patristic distances and compared the correlation coefficient to the distribution of correlation coefficients from a null model generated by randomizing the species across the phylogeny 1000 times in order to shuffle the patristic distance scores. 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.

Phenotypic repulsion and attraction

Traits and habitat features important for environmental filtering are likely to be associated with the degree of niche overlap and co-occurrence among species (Webb et al. 2002). Pairwise trait differences between species were correlated with pairwise niche overlap and co-occurrence scores to determine whether there was evidence for

phenotypic repulsion or attraction (Webb et al. 2002). Phenotypic attraction would be indicated by a trait for which there were a significant negative correlation between the pairwise trait differences and niche overlap or co-occurrence (i.e., co-occurring species have a high degree of phenotypic similarity). Phenotypic repulsion would be indicated by a positive correlation between trait differences and co-occurrence (Cavender-Bares and Wilczek 2003). Traits that show significant repulsion may be important in preventing species sharing those traits from co-occurring. Significance levels were determined by comparing the observed correlation coefficients for trait differences vs. co-occurrence or vs. niche overlap to the distribution of correlation coefficients generated in the null model from either basal area or presence/absence of oak species within plots.

Results

Phylogenetic analysis

Four most parsimonious trees were found (one is shown in Figure 3a) whose topology was consistent with previously published phylogenies of oaks (Manos et al. 1999; Manos et al. 2001; Manos and Stanford 2001), a summary of which is shown in Fig. 3b. Analysis of multiple accessions from individual species (data not shown), showed little evidence of reticulation among distantly related species, in contrast to previous studies of oaks (Whittemore and Schaal 1991; Dumolin-Lapegue 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 1997).

Ecological filtering and phylogenetic attraction

Results of the MANOVAs (Table 1) show no evidence for niche conservatism in terms of spatial distribution or habitat factors within the two (red and white+live) or three (red, white, live) major phylogenetic lineages of oaks represented in Florida. Thus, members of clades do not cluster together spatially or in terms of habitat preferences. On the other hand, three major community affiliations based on floristic descriptions of

species significantly explain much of the variance in both spatial distribution and habitat preferences of species (see also Cavender-Bares et al. submitted). While this latter result might be expected, it clearly indicates that species distributions are not random with respect to the abiotic environment and provides evidence for ecological filtering. Both community affiliation and phylogenetic lineage significantly explain the variance among various functional traits. However, those traits that distinguish major oak lineages are not traits that show a correlation with habitat type (bottom of Table 1). Including three clades (red, white, and live) explained more of the total variation in traits than only two clades (red and white+live) because leaf level traits, including SLA and leaf lifespan are differentiated between white and live oaks with white oaks having thinner, short-lived leaves and live oaks having thicker, longer-lived leaves. This provides initial evidence that closely related species do not show phylogenetic attraction in terms of habitat and distribution. It also demonstrates that while some traits are conserved within clades, these traits are not the same as those that are shared among members of a given community.

Independent contrast correlations

Independent contrasts provide strong evidence for correlated evolution in functional traits and habitat preferences; unless otherwise stated, all correlations discussed here are based on independent contrasts using the ITS phylogeny. 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 optimal conditions in a glasshouse, were positively correlated with soil moisture preferences (Fig. 4 a,b). Maximum hydraulic conductance of mature trees, percent loss of conductivity, vessel diameters and seedling growth rate were also correlated with soil moisture preferences (Table 2). Radial growth rates of mature trees, and seedling growth rates were positively correlated with soil fertility (exchangeable nitrate+ammonium)(Fig. 4 c,d), 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 2). With respect to fire regime, outer bark thickness of saplings, the life stage most susceptible to

ground fires, was negatively correlated with the ranked index of fire return interval (inverse of fire frequency) (Fig. 4e). Note that this ranking excludes scrub species associated with severe and relatively frequent fires. These species actually have thinner bark than the sandhill species found where fire frequency is higher but fire severity is lower. Scrub fires tend to be so severe that bark offers little protection. In contrast, these species are short-statured and have a high rhizome resprouting potential. A clear trade-off can be seen between rhizome resprouting potential and asymptotic height (Fig. 4f). 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 2).

In hammock and sandhill environments, height (and rapid height extension, i.e., growth) offers 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 invest less in mechanisms that allow them to recover after severe fire. In contrast, species that experience severe fire regimes invest less in aboveground biomass and stature and more in mechanisms of rapid recovery after fire. While a number of traits were strongly correlated with habitat preferences, other traits, such as leaf lifespan and acorn maturation time, showed no correlation with soil moisture, soil fertility or fire regime (Table 2).

Phylogenetic structure of communities

Habitat convergence--We found that Floridian oak species show a tendency towards habitat convergence, illustrated by the negative relationship between critical habitat features and phylogenetic distance. In particular, there was a significant negative correlation between divergence in soil moisture preference and phylogenetic distance relative to the null model (Table 3). Thus, distantly related species share more similar habitats, and closely related species share more contrasting habitats than expected by chance. This can be visualized by mapping mean soil moisture values of species habitats onto a phylogeny (Fig. 4). 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.

Co-occurrence and niche overlap vs. phylogenetic distance--In a second analysis, we found that co-occurrence, calculated from basal area of oaks within plots, was significantly positively correlated with phylogenetic distance (Figure 6), relative to a null model. This result was robust to tree topology (Table 4) and branch length calculation method (not shown). The relationship was also significant if the basal area matrix was randomized rather than the phylogeny (not shown). 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 repulsion of closely related oak species, and shows that within the genus, phylogenetic attraction is not occurring. The same result was marginally significant (P = 0.07) if co-occurrence was calculated from presence/absence rather than from basal area.

We ran the same test correlating pairwise niche overlap values with phylogenetic distance and the results were similar. When niche overlap was calculated from the basal area matrix, niche overlap was more positively correlated with phylogenetic distance than expected based on the null model of species randomly distributed across the phylogeny (P = 0.01). When niche overlap was calculated from presence/absence, the same trend was apparent but not significant (P = 0.187). Again, these results were robust to tree topology (Table 4) and branch length method (not shown).

Niche overlap at different phylogenetic scales--Niche overlaps of all pairwise combinations of species within each of the two major lineages (red oaks and white+live oaks) showed significantly less overlap than expected by chance, indicating that within both clades species are partitioning the soil moisture gradient (bottom half of Table 5). These results can be visualized for distributions of red oak species (Fig. 7a) and white+live oak species (Fig. 7b), respectively, across the soil moisture gradient. Species within the white oak s.s. clade also showed significantly less overlap than expected (Table 5). Live oaks did not show less overlap than expected, although the two most abundant live oaks, *Q. virginiana* and *Q. geminata*, did show significant habitat partitioning if niche overlap was calculated from presence/absence (P = 0.041) but this

trend was only marginally significant if calculated from basal area (P = 0.066). When the analysis was done at different phylogenetic levels by cumulating the abundances of taxa within clades (for basal area) or scoring occurrences at the clade level (for presence/absence), overlap at the highest phylogenetic level (deepest node) showed that the red oak group overlaps with the white+live oak group significantly more than expected by chance if calculated from basal area (P = 0.011), and the overlap was marginally significant if calculated from presence/absence (P = 0.105; Table 5). Combined, these results indicate that niche partitioning is occurring among taxa at the lowest phylogenetic scale, i.e., at the species level, so that closely related species occur in contrasting habitats. The highest degree of niche partitioning between lineages is actually occurring at intermediate phylogenetic scales at a depth of 2 and 3 nodes. This result arises because some of the most recent (shallowest) 2 and 3 member clades comprise species that do not partition the soil moisture gradient more than expected if their distributions were random (e.g., *Q. falcata and Q. laevis* or *Q. hemispherica, Q. nigra* and *Q. laurifolia*). At the highest phylogenetic level, there is more overlap than expected because niche radiation into all possible soil moisture environments has occurred within both of the major clades. Thus, distribution of taxa within the red oak lineage mirrors the distribution of taxa within the white+live oak lineage. This phenomenon can be viewed in Fig. 7. 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.

The same analyses were carried out to investigate whether taxa were overdispersed with respect to their degree of co-occurrence. In general, these results are similar to those described for niche overlap. In this case, we found that at the individual species level within the white+live oak clade and also within the white oaks s.s., species co-occurred less often than expected. Within the red oak clade, however, this was not the case (Table 5). The lack of overdispersion arises largely because two red oaks, *Q. falcata* and *Q. laevis* occur together more often than expected when presence/absence is used to calculate co-occurrence, although not when basal area is used because it provides higher resolution of species distributions than presence/absence since it is a measure of relative

abundance. If only one of these species is included, or if they are combined as one taxon, overdispersion within the red oaks is higher than expected (not shown). These two species also co-occur to some extent with *Q. incana*. If mean species co-occurrences is calculated for the clade one node higher to exclude *Q. incana*, overdispersion is again greater than expected within the red oaks (Table 7). The highest degree of overdispersion within the red oaks occurs at the intermediate phylogenetic scale, i.e., at the 3rd node when *Q. falcata*+*Q. laevis* are compared to *Q. nigra*+*Q. hemispherica*+*Q. laurifolia.* At the deepest node, we again find that the red oak group and the white+live oak group show a higher degree of co-occurrence than expected by chance (Table 5). 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.

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 6). Acorn maturation time, vulnerability to freezing, wood density and average vessel diameters were significantly conserved. Leaf lifespan (maximum) and specific leaf area also showed a tendency towards conservatism. No traits were significantly convergent, although, it is statistically very difficult for trait values to be more convergent than a random distribution. A negative correlation coefficient, in effect, indicates some degree of convergence in the trait. These results are consistent with other measures of trait convergence/conservatism, including the Quantitative Convergence Index (QVI) (Ackerly and Donoghue 1998) (data not shown).

Phenotypic attraction and repulsion

Several traits showed higher phenotypic attraction than expected, indicating that co-occurring species were phenotypically similar. These include bark thickness, radial growth rate, rhizome resprouting potential, whole shoot transpiration and maximum hydraulic conductance, as indicated by a more negative than expected correlation coefficient for trait divergences vs. co-occurrence or niche overlap (Table 7). These traits are closely linked to fire regime, soil moisture and fertility, as shown in Fig. 3 and Table

2, and are likely to be important in the ecological sorting of species. Other traits, including acorn maturation time, vulnerability to freezing, average and/or maximum leaf lifespan, and first year vessel diameters, show higher phenotypic repulsion than expected, as indicated by a more positive than expected correlation for trait divergence vs. co-occurrence or niche-overlap (Table 7). Of these traits, several are either significantly or relatively conserved, including acorn maturation time, vulnerability to freezing, first year vessel diameter and max. leaf lifespan. Their potential significance with respect to co-existence is addressed below.

Discussion

Floridian oak communities can be classified into three major community types, hammock, sandhill and scrub woodland, based on fire frequency and intensity and soil moisture and fertility (Kurz 1942; Laessle 1958; Kurz and Godfrey 1962; Myers 1990; Cavender-Bares et al. submitted). Ordination analysis of vegetation show that individual oak species tend to be concentrated in one of these three community types (Cavender-Bares et al. submitted). Multiple analysis of variance of axes scores from the ordination analysis and of critical soil habitat factors show that these community types significantly explain the variance in both the distribution of species and in the abiotic environment. Further, the ecophysiological data show a close correspondence between the community type in which a species is usually found and traits that would seem likely to promote survival and reproduction in that community type. This can be seen for traits related to growth and competitive ability, fire tolerance and drought stress in the MANOVA of traits. Independent contrast correlations also show strong evidence for correlated evolution of critical functional traits and habitat factors. For example, contrast correlations show that whole shoot transpiration (Fig. 3a), maximum hydraulic conductance and seedling absolute growth rate (Fig. 3d) are positively correlated with species soil moisture and soil fertility preferences (Table 2). 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. Indeed, most of these traits show high phenotypic attraction (Table 7). Taken together, these data show

that within a habitat, co-occurring species show similarities in traits that are likely to be critical to their survival in the abiotic environment, providing evidence for the ecological filtering hypothesis. Given these phenotypic similarities, and the general assumption that closely related species will be more similar, one might predict that co-occurring oaks will be phylogenetically clustered.

However, MANOVA results show no evidence of habitat conservatism or clustering based on lineage (Table 1). In contrast, three separate analyses demonstrate a pattern of phylogenetic repulsion among congeneric oak species in this landscape. First, distantly related oak species show convergence in critical habitat features when tested against null models (Table 3). In particular, soil moisture preferences of species are significantly more convergent than expected (Fig. 5). 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. 6, Table 4). 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 pattern is most significant within the white oaks s.s., but is also significant among red oaks and between two of the three live oaks (Table 5). At the deepest node between red oaks and the white+live oaks, the cumulative distribution of species within these two clades shows more overlap than expected (Fig. 7). This pattern arises because species have expanded into all possible niches within each of these two major clades. A similar result is obtained when the degree of co-occurrence is examined at different depths in the phylogeny. These results clearly show that within the oak genus, there is no evidence for niche conservatism, corroborating the MANOVA results shown in Table 1. In contrast, closely related species are less likely to occur together or in similar habitats 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 noted but never explained (Mohler 1990).

We explain the phylogenetic repulsion in the assembly of Floridian oak communities first by a high degree of convergence in ecologically important physiological and morphological traits. Indeed, traits that correlate closely with habitat

factors, such as soil moisture and fire regime, tend to be convergent. Patterson and Givnish (2002) showed a similar pattern of convergence in multiple traits among species in different lineages that share the same set of ecological conditions. In this study, seedling absolute growth rate, asymptotic height, rhizome resprouting potential, and whole shoot transpiration show relatively high evolutionary convergence (Table 6), and all of these traits are significantly correlated with critical habitat features using phylogenetically independent contrasts (Fig. 4, Table 2). Oak species that are phenotypically similar with respect to convergent traits also show higher niche overlap than expected as indicated by a negative correlation between trait divergence and niche overlap (Table 7); thus, species with similar niches have similar trait values for those traits that are convergent. We also show that co-occurring species have similar trait values, as indicated by a negative correlation between trait divergence and co-occurrence for the most convergent traits (Fig. 7). These observations suggest the generalization that clades that include multiple, co-occurring species must have sufficient evolutionary potential to be able to move fluidly, in evolutionary time, along the gradient of ecophysiologically relevant environmental variation.

At the same time, conserved traits may prevent closely related species from co-occurring and may promote the co-occurrence of less closely related species through mechanisms of complementarity. Due to the pattern of phylogenetic repulsion of these oaks in natural communities, any trait that differentiates the major lineages of oaks will show significant phenotypic repulsion, as indicated by a negative relationship between trait divergence and species co-occurrence.

Acorn maturation time is a possible candidate for a trait that may be responsible for phenotypic repulsion, and it does not seem important in ecological filtering as suggested by a lack of correlation with habitat variables (Table 2). Acorn maturation times are highly conserved at the lineage level, one year in white and live oaks, two years in red oaks (Nixon 1997), which might promote temporal or spatial segregation via storage mechanisms (Chesson and Warner 1981; Chesson 1985). 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 timing of

regeneration could be staggered as a result of climatic variability, increasing the likelihood of co-occurrence between red and white oaks.

Similarly, there is evidence that red oaks are more susceptible to oak wilt (*Ceratocystis fagacearum)* than white oaks s.s. (Farr et al. 1989; Bruhn et al. 1991) , which could potentially be linked to conserved differences in wood anatomy. If pathogens tend to show conservatism of host-specificity, white oak species co-occurring with red oaks would tend to suffer less pathogen-mediated mortality than would a co-occurring red oak. The same might be true for mortality resulting from seed predation. 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) is likely to give rise to common seed predators among red oaks and among white oaks, respectively (Smallwood et al. 2001). Such traits that are conserved within lineages could result in density-dependent interactions with organisms of other trophic levels, preventing co-occurrence of closely related species and promoting the co-occurrence of distantly related species. Such hypotheses are empirically testable and are an exciting area for further research.

While we find a number of cases where convergent traits show phenotypic attraction and conserved traits show phenotypic repulsion, some conserved traits show evidence for phylogenetic attraction and for correlated evolution with habitat preferences. Both vessel diameter and wood density are conserved traits, with white oaks having smaller vessels and denser wood (live oaks have even denser wood) than red oaks. Within each clade, however, both of these traits are correlated with soil moisture to some extent (Table 2). In contrast, some traits that may be expected to be correlated with habitat factors based on theoretical considerations are not. For example, there is no clear correlation between leaf longevity and nutrient availability (Table 2), a relationship that is predicted to be negative based on theoretical models of leaf construction costs and nutrient use efficiency (Kikuzawa 1991; Reich et al. 1991; Givnish 2002). Given that multiple traits are inextricably linked for developmental or architectural reasons (Gould and Lewontin 1979), plants may only be able to track environments well enough to optimize the most critical traits for survival and reproduction (Ackerly 2003).

Interestingly, rather than showing phenotypic attraction, maximum leaf lifespan actually shows significant phenotypic repulsion (Table 7), such that co-occurring oaks are more likely to have contrasting phenology than expected. 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 and potentially reducing competition between species with contrasting phenologies (Sakai 1992). It may be that within this system, species with contrasting resource use strategies may be more able to increase total ecosystem nutrient use efficiency than species with similar strategies, thus promoting their co-occurrence and increasing the number of species that can coexist.

Hybridization among closely related species may be another possible explanation for the low level of co-occurrence among closely related congeners. Speciation may not be able to occur sympatrically due to introgression. Thus, genetic differentiation may only have occurred in allopatry as a result of contrasting niche specialization. While the pattern of phylogenetic repulsion we have demonstrated presents the possibility of parallel adaptive radiation into contrasting niches, we cannot make any conclusive statements about the speciation process due to the high number of intervening taxa in the phylogeny that are not components of this ecosystem. The apparent pattern of adaptive radiation could disappear in a more complete phylogeny. Understanding the ecology of Floridian oaks in the context of a more complete phylogeny is the subject of ongoing research (Cavender-Bares, in preparation).

Our study shows that phylogenetic repulsion is occurring among Floridian oaks and demonstrates that this phenomenon is dependent on the scale of phylogenetic analysis. The dominance of these forests by oaks, as a whole, presumably reflects shared traits amenable to broad-scale environmental conditions. But at smaller spatial scales, co-occurring oak species are more distantly related than expected, relative to other members of the genus. This non-random phylogenetic pattern of community assembly may be the result of greater ecological complementarity (minimizing competition) and reduced density dependent mortality of more distantly related oaks. However, the

abundance of oak species at each site depends on the phylogenetic scale of trait evolution. Traits that vary most readily at low phylogenetic scales are those that are critical for lineages to switch between available community types. In contrast, traits that are more heavily conserved, and which 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 types of trait evolve.

Acknowledgements

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Table 1
MANOVA results testing whether communities (sandhill,scrub and hammock) or phylogenetic lineages (red and white oaks or red, white, and live oaks), treated as main fixed effects, significantly explain the variance among the following groups of dependent variables: 1) first and second axis scores for oak species from detrended correspondence analysis of occurrences of all woody species within random plots, 2) habitat factors, including soil moisture, organic matter content, exchangeable phosphorus, exchangeable nitrate and ammonium, pH, and calcium content; and 3) functional traits, including sapling outer bark thickness, average vessel diameter of second year wood, maximum leaf lifespan, specific leaf area (SLA), percent loss of hydraulic conductivity (PLC), wood density, radial growth rate, rhizome resprouting potential, asymptotic height, acorn maturation time, and whole shoot transpiration normalized by sapwood area. Main effects are shown in bold if P =< 0.05. For the MANOVAs of traits, overview P values are shown for individual traits.

MANOVA	**Main effect**	**Lambda**	**Prob**	**Approx**	**df**	**err df**
DCA axes scores						
	Const	0.187	0.000	23.9	2	11
	Clades (Red, White)	0.823	0.343	1.18	2	11
	Const	0.202	0.000	21.8	2	11
	Clades (Red, White, Live)	0.939	0.949	0.176	4	22
	Const	0.059	0.000	80.1	2	10
	Community	0.097	**0.000**	11.1	4	20
Habitat factors						
	Const	0.002	0.000	871	6	10
	Clades (Red, White)	0.820	0.885	0.366	6	10
	Const	0.002	0.000	808	6	9
	Clades (Red, White, Live)	0.477	0.757	0.672	12	18
	Const	0.001	0.000	1,180	6	9
	Community	0.081	**0.006**	3.78	12	18
Traits						
	Const	0.000	0.000	4,010	11	5
	Clades (Red, White)	0.089	**0.052**	4.63	11	5
	Const	0.000	0.000	18,700	11	4
	Clades (Red, White, Live)	0.003	**0.004**	6.91	22	8
	Const	0.000	0.000	3,910	11	4
	Community	0.006	**0.021**	4.23	22	8

Table 1 (cont'd)

Overview p-values for individual traits

	Community	Clades (Red, White)	Clades (Red, White, Live)
df	2	1	2
Wilk's Lambda	**0.02**	**0.05**	**0**
Sapling outer bark	**0**	0.89	0.17
Vessel diam (yr 2)	0.40	**0.03**	**0.03**
Leaf lifespan (max.)	0.10	0.82	**0.05**
SLA	0.25	0.26	**0**
PLC	0.07	0.58	0.65
Wood density	0.07	**0**	**0**
Radial growth	**0**	0.27	0.46
Rhizome resprouting potential	**0**	0.78	0.8
Asymptotic height	**0**	0.82	0.89
Acorn maturation time	0.94	**0**	**0**
Whole shoot transpiration	0.21	0.58	0.17

Table 2.
Independent contrast correlation coefficients for functional traits in relation to environmental factors. Correlation coefficients > 0.6 are shown in bold. HKYclock branchlengths were used but results were similar for all tree topologies and branchlength calculation methods.

Traits	Soil moisture Vol. H_2O (Vol. soil)$^{-1}$	Soil fertility NH_4+NO_3 (mg kg^{-1})	Fire return interval (index)	Fire severity (index)
Acorn maturation time	-0.024	-0.013	-0.088	0.088
Vulnerability to freezing	0.050	0.455	-0.224	-0.551
SLA	0.069	-0.117	-0.442	0.015
Seedling relative growth rate	0.127	0.410	0.323	-0.428
Leaf lifespan (ave.)	-0.390	-0.005	0.377	0.401
Leaf lifespan (max.)	-0.393	-0.082	0.334	0.135
Wood density	-0.418	-0.453	0.048	0.329
Year 1 vessel diam	0.501	0.188	-0.174	-0.092
Sapling outer bark thickness	-0.347	-0.209	**-0.920**	-0.037
Asymptotic height	0.354	**0.785**	0.564	**-0.833**
Radial growth rate	0.533	**0.784**	**0.672**	**-0.685**
Rhizome resprouting potential	**-0.633**	**-0.824**	**-0.639**	**0.840**
Percent loss of conductivity	**0.670**	**0.650**	0.557	**-0.641**
Year 2 vessel diam	**0.679**	0.353	**0.672**	-0.303
Hydraulic conductance (max.)	**0.759**	0.408	**0.717**	-0.223
Whole shoot transpiration	**0.827**	**0.622**	0.433	-0.451
Seedling canopy transpiration rate	**0.841**	**0.807**	**0.742**	-0.525
Seedling absolute growth rate	**0.881**	**0.867**	**0.813**	**-0.608**

Table 3.

Correlation coefficients for the relationship between differences in habitat preferences among species pairs and the patristic distances between species pairs. A positive correlation indicates habitat conservatism while a negative correlation indicates habitat convergence. All habitat factors show a negative correlation, indicating a lack of habitat conservatism. Soil moisture regime shows more convergence than would be expected if species were randomly distributed. In contrast, the northern range limit, although not conserved, shows a tendency for closely related species to share climatic distributions

	r value	sim>obs	obs>sim
Northern range limit	0.019	275	725
Exchangeable phosphorus	-0.005	479	521
Fire regime	-0.045	628	372
Calcium content	-0.036	636	364
pH	-0.034	659	341
Exchangeable NH_4+NO_3	-0.067	857	143
Organic matter content	-0.080	924	76
Soil moisture	-0.092	**970**	30

Habitat conservatism

Habitat convergence

Table 4.
Correlation coefficients for the degree of co-occurrence or niche overlap (calculated based on basal area or presence/absence of oak species within plots) vs. phylogenetic distances between species. Correlations were calculated for four tree topologies using HKY clock branchlengths. Observed values were compared to a null with 1000 randomizations. A more positive correlation than expected (obs>sim) indicates phylogenetic repulsion while a more negative correlation than expected would indicate phylogenetic attraction. Niche overlap was calculated for seven levels of soil moisture.

		Co-occurrence		Niche overlap	
		(basal area)	(pres./abs.)	(basal area)	(pres./abs.)
Tree 1	r value	0.140	0.113	0.111	0.065
	sim>obs	40	70	10	177
	obs>sim	**960**	930	**990**	823
Tree 2	r value	0.140	0.113	0.118	0.064
	sim>obs	35	82	27	189
	obs>sim	**965**	918	**973**	811
Tree 3	r value	0.136	0.108	0.118	0.056
	sim>obs	47	88	36	244
	obs>sim	**953**	912	**964**	756
Tree 4	r value	0.138	0.111	0.116	0.058
	sim>obs	26	81	26	249
	obs>sim	**974**	919	**974**	751

Table 5. Results of randomization tests for co-occurrence and niche overlap at different phylogenetic scales. In the top half of the table, normalized cumulative abundances of species at higher taxon levels were compared at phylogenetic noes of increasing depth (deepest node shonw first) based on Fig. 2. Number of simulations in which observed values were less than, greater than or equal to expected is shown. Significant tests are shown in bold. Significant results in which observed niche overlap between species or taxon pairs was less than expected can be interpreted as niche partitioning and phylogenetic repulsion of taxa, while tests showing niche overlap > expected indicate phylogenetic attraction. Likewise, for tests of co-occurrence, observed overlaps between species or taxon pairs less than expected can be interpreted as overdispersion or phylogenetic repulsion while values greater than expected indicate underdispersion of taxa or phylogenetic attraction.   Co-occurrence was calculated as Schoener's similarity index and niche overlap was calculated as Pianka's niche overlap (see text). These indices were calculated from both basal area (BA) and presence/absence (P/A) of oaks within plots and compared to null models. In the null model based on basal area, the proportion of basal area in each plot was shuffled across all of the plots for each species, constraining total basal area per species. In the null model based on presence/absence, the raw presence/absence data of species within plots was randomized, constraining total occurrences of each species and the number of species per plot. For higher taxa, relative basal area of each member species was summed.   Presence or absence of higher taxa were only scored once per plot, regardless of how many species per taxon occurred in the plot. In the bottom half of the table, results of tests for means of pairwise niche overlap and co-occurrence values for all possible species pairs within decreasingly inclusive clades are shown. N indicates the number of species within the clade.

Phylogenetic depth	Taxa	niche overlap (BA)			niche overlap (P/A)			co-occurrence (BA)			co-occurrence (P/A)		
		obs<sim	obs>sim	obs=sim	obs<sim	obs>sim	obs=sim	obs<sim	obs>sim	obs=sim	obs<sim	obs>sim	obs=sim
Deep 6 nodes	Red oaks v White + Live oaks	11	**989**	0	105	895	0	2	**998**	0	4	**996**	0
5 nodes	FA+LV+HE+NI+LA+MY+PM+SH v IN	562	438	0	850	150	0	24	**976**	0	453	547	0
	White s.s. v Live	823	177	0	937	63	0	912	88	0	**966**	34	0
4 nodes	FA+LV+HE+NI+LA v MY+PM+SH	755	245	0	377	623	0	649	351	0	397	603	0
	ST+MA+AU+CH v MX	192	808	0	**991**	9	0	603	397	0	899	101	0
3 nodes	FA+LV v HE+NI+LA	**1000**	0	0	**1000**	0	0	**1000**	0	0	985	15	0
	MA+AU+CH v ST	**994**	6	0	**995**	5	0	**993**	7	0	572	428	0
2 nodes	HE+NI v LA	494	506	0	311	689	0	752	248	0	195	805	0
	MY+PM v SH	**1000**	0	0	**998**	0	2	600	0	400	944	5	51
	AU+CH v MA	898	102	0	**995**	5	0	**988**	12	0	886	110	4
	GE+MN v VI	691	309	0	**956**	44	0	783	217	0	873	127	0
Shallow 1 node	FA v LV	200	800	0	88	912	0	773	227	0	3	**978**	19
	HE v NI	**979**	21	0	922	78	0	**952**	48	0	514	486	0
	PM v MY	852	0	148	813	0	187	291	0	709	696	0	304
	AU v CH	648	352	0	418	582	0	556	0	444	**1000**	0	0
	GE v MN	781	219	0	551	449	0	248	752	0	46	**954**	0
	GE v VI	934	66	0	**959**	41	0	526	474	0	114	886	0
	VI v MN	461	539	0	546	454	0	605	0	395	445	528	27

Means of species pairs within clades		obs<sim	obs>sim	obs=sim	obs<sim	obs>sim	obs=sim	obs<sim	obs>sim	obs=sim	N	obs<sim	obs>sim	obs=sim
5 nodes	Red oaks	**1000**	0	0	**1000**	0	0	914	86	0	9	198	802	0
	White + Live oaks	**1000**	0	0	**1000**	0	0	**1000**	0	0	8	**994**	6	0
4 nodes	FA, LV, HE, NI, LA, MY, PM, SH	**1000**	0	0	**1000**	0	0	**1000**	0	0	8	631	369	0
	White oaks s.s.	**1000**	0	0	999	1	0	**992**	8	0	5	**994**	6	0
3 nodes	FA, LV, HE, NI, LA	**1000**	0	0	**1000**	0	0	**1000**	0	0	5	982	18	0
	ST, MA, AU, CH	**998**	2	0	**998**	2	0	**1000**	0	0	4	995	5	0
2 nodes	HE, NI, LA	931	69	0	336	664	0	**971**	29	0	3	306	694	0
	MY, PM, SH	**1000**	0	0	**1000**	0	0	792	0	283	3	**995**	0	5
	MA, AU, CH	**960**	40	0	943	57	0	**993**	7	0	3	**990**	10	0
	Live oaks	922	78	0	829	171	0	670	330	0	3	122	878	0

Taxon codes are as follows: **AU** (*Q. austrina*), **CH** (*Q. chapmanii*), **FA** (*Q. falcata*), **GE** (*Q. geminata*), **HE** (*Q. hemispherica*), **IN** (*Q. incana*), **LA** (*Q. laurifolia*), **LV** (*Q. laevis*), **MA** (*Q. margaretta*), **MN** (*Q. minima*), **MX** (*Q. michauxii*), **NI** (*Q. nigra*), **PM** (*Q. pumila*), **SH** (*Q. shumardii*), **ST** (*Q. stellata*), **VI** (*Q. virginiana*); **Red oaks** (FA, HE, IN, LA, LV, NI, PM, SH); **White oaks** s.s.(AU, CH, MA, MX, ST), **Live oaks** (GE, MN, VI); **White s.s.+Live oaks** (latter two groups combined).

Table 6.
Correlation coefficients for pairwise trait differences among species pairs and patristic distances between them. A more positive correlation than expected indicates trait conservatism while a negative correlation indicates convergent evolution of traits. Several traits show more conservatism than expected although no traits show more convergence than random based on a null model in which species' trait values are randomized across the phylogeny.

		r value	sim>obs	obs>sim
Trait conservatism	Acorn maturation time	0.747	0	**1000**
	Wood density	0.383	0	**999**
	Vulnerability to freezing	0.273	3	**997**
	Vessel diameter (ave. yr 2)	0.190	17	**983**
	Vessel diameter (ave. yr 1)	0.048	154	846
	SLA	0.081	110	890
	Max. leaf lifespan	0.009	328	672
	Sapling outer bark thickness	-0.001	364	636
	Radial growth	-0.004	392	608
	Hydraulically weighted vessel d	-0.005	408	592
	Max. hydraulic conductance	-0.018	478	522
	Seedling relative growth rate	-0.001	505	495
	Ave. leaf lifespan	-0.020	562	438
	Whole shoot transpiration	-0.042	664	336
Trait convergence	Seedling absolute growth rate	-0.086	748	252
	Asymptotic height	-0.059	792	208
	Rhizome resprouting potential	-0.068	821	179
	PLC	-0.067	866	134

Table 7

Correlation coefficients for pairwise trait differences among species pairs and co-occurrence or niche overlap values between species pairs. A more negative correlation coefficient than expected based on the null model (obs<sim) indicates that species that co-occur or whose niches overlap have similar traits (phenotypic attraction). A more positive correlation than expected (obs>sim) indicates that overlapping species have greater differences in trait values than expected (phenotypic repulsion). Correlation coefficients were compared to that of a distribution of 1000 correlation coefficients generated by randomizing the raw data matrix from which niche overlap is calculated. Basal area of each species was randomized across the plots, constraining the total basal area per species. Table shows the number of simulated matrices that give greater or lower correlation coefficients than the observed matrix. Co-occurrence and niche overlap values were calculated based on basal area of oak species within plots or on presence/absence; niche overlap values were calculated across 7 soil moisture levels. See text for details.

| | | co-occurrence (basal area) | | | co-occurrence (P/A) | | | niche overlap (basal area) | | | niche overlap (P/A) | | |
	Trait	r	obs<sim	obs>sim	r	obs<sim	obs>sim	r	obs<sim	obs>sim	r	obs<sim	obs>sim
Phenotypic repulsion	Acorn maturation time	0.19	1	**999**	0.1287	21	**979**	0.12	10	**990**	0.0883	113	887
	Vulnerability to freezing	-0.206	1	**999**	-0.258	0	**1000**	-0.04	23	**977**	-0.118	0	**1000**
	Max. leaf lifespan	0.143	14	**986**	0.0619	234	766	0.055	154	846	0.0787	231	769
	Ave. leaf lifespan	0.022	23	**977**	-0.0853	21	**979**	-0.02	81	919	-0.001	29	**971**
	Vessel diameters (ave. year 1)	-0.004	40	**960**	-0.1148	0	**1000**	-0.15	44	**956**	-0.268	0	**1000**
	Seedling relative growth rate	0.068	149	851	0.0241	385	615	0.064	239	761	-0.03	518	482
	SLA	0.061	211	789	0.0074	892	108	0.1	178	822	0.0116	847	153
	Seedling absolute growth rate	-0.087	477	523	-0.0263	558	442	-0.2	888	112	-0.151	779	221
	Vessel diameters (ave. year 2)	-0.042	531	469	-0.0949	743	257	0.003	342	658	-0.016	395	605
	Wood density	0.145	558	442	0.0429	926	74	0.033	545	455	-0.014	552	448
	PLC	-0.074	567	433	-0.1137	540	460	-0.21	936	64	-0.214	809	191
	Max hydraulic conductance	0.048	536	464	0.0027	**958**	42	-0.08	902	98	-0.037	**955**	45
	Hydraulically weighted vessel d.	0.089	693	307	0.1034	**1000**	0	0.146	478	522	0.1851	568	432
	Whole shoot transpiration	-0.062	768	232	-0.0665	**973**	27	-0.19	**971**	29	-0.109	915	85
	Asymptotic height	-0.34	808	192	-0.3915	735	265	-0.31	878	122	-0.417	912	88
Phenotypic attraction	Sapling outer bark thickness	-0.195	**997**	3	-0.256	**1000**	0	-0.15	**974**	26	-0.276	**995**	5
	Radial growth	-0.228	**1000**	0	-0.2294	**1000**	0	-0.18	**981**	19	-0.216	**980**	20
	Rhizome resprouting potential	-0.422	**1000**	0	-0.4194	**1000**	0	-0.41	**997**	3	-0.434	**987**	13

Figure legends

Figure 1.

Histogram of the number of oak species per plot over 74 random 0.10 ha plots in three state preserves in North Central Florida. Note that 80% of the plots have three species or more.

Figure 2.

Matrix of four data sets on the floridean oaks, including their spatial distribution, their abiotic environment, mean values for phenotypic traits, and phylogenetic relationships between species. Each of these data sets can be examined in relation to the other data sets to reveal patterns in species assemblages within communities, using the tests shown in the top-right half of the matrix.   Tests using null models are given in bold and possible interpretations of these tests are shown below. In the bottom left half of the matrix, the traditional domains of each kind of analysis are given. By combining four kinds of data sets, each traditionally used in different fields of biology, new insights can be brought to community ecology and evolutionary biology.

Figure 3.

A) Phylogenetic reconstruction of 17 species of sympatric oaks in northern central Florida (one of four most parsimonious trees). Bootstrap values above 50% are given in large numbers above branches. There is strong support for three major clades, red oaks, white oaks and live oaks. White oaks (Quercus s.s.) and live oaks (Virentes) combined form a clade sister to the red oaks. Branch length distances (HKY clock) are shown below branches. B) A summary of the Quercus genus phylogeny from P. Manos and colleagues from Manos et al (1999), Manos and Sanford (2001), and Manos et al. (2001).

Figure 4.

Independent contrast correlations using the tree topology shown in Fig. 3 and HKY branchlengths. Correlations between contrasts in species traits and contrasts in species

habitat preferences provide evidence for environmental filtering because they show that species occur in the habitats for which their traits are well suited. A) Contrasts in transpiration normalized by sapwood area vs. contrasts in soil moisture preferences.   B) Contrasts in whole canopy transpiration rates of seedlings grown in a common garden vs. contrasts in soil moisture preferences.   C) Contrasts in radial growth of mature trees vs. contrasts in soil fertility preference (measured as exchangeable ammonium + nitrate concentration). D) Contrasts in seedling absolute growth rate from seedlings grown in a common garden vs. contrasts in soil fertility preferences of mature trees in the field. E) Contrasts in thickness of sapling outer bark vs. contrasts in a ranked index of fire return interval (see text). F) There is a tradeoff between asymptotic height and rhizome sprouting potential as shown by the significant negative contrast correlation between these traits. In habitats where the fire regime is very severe, species have a high capacity to resprout from rhizomes and spread clonally but invest little in height growth. In contrast, in habitats where the fire regime is not severe and crown fires are unlikely, species achieve tall stature but have a reduce capacity to recover from severe fires. All correlations were robust to other branchlength methods and other tree topologies. Different symbols are shown for contrasts within the Red, White, and Live clades as well as for contrasts between two clades.

Figure 5.

Mean soil moisture values of species' habitats are mapped on the phylogeny shown in Fig. 3. Dark shades indicate wet habitats while light colors indicated dry habitats. It is apparent that within both the red oak and white+live oak clades, species occupy wet, dry, and mesic habitats. Indeed, pairwise differences in soil moisture preferences are significantly negatively correlated with pairwise genetic distances, indicating that species show higher convergence in soil moisture preference than expected based on a null model in which species are randomized across the phylogeny (see Table 3).

Figure 6.

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
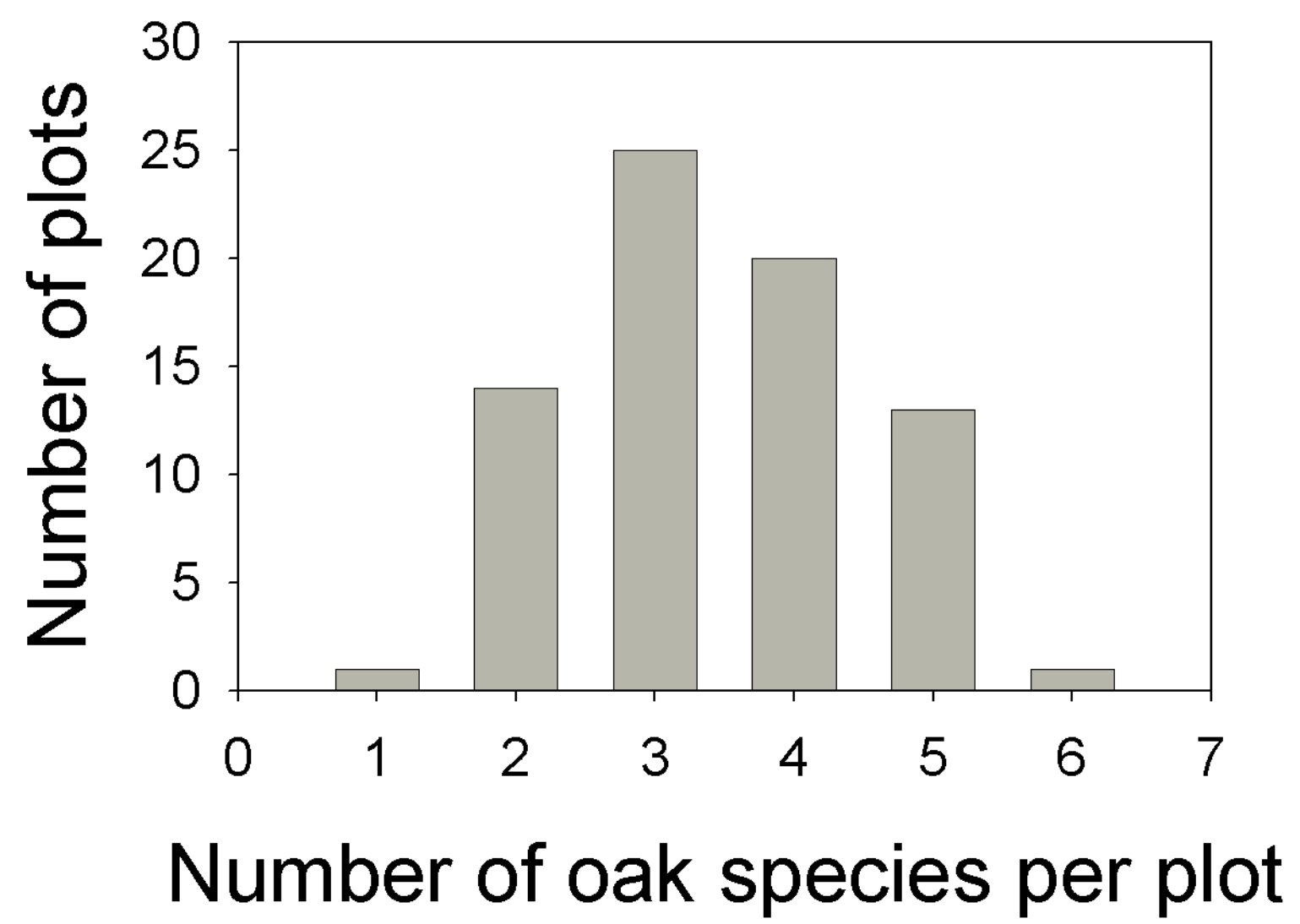
(CI), calculated from basal area of oak trees within plots, and phylogenetic distance when compared to a null model in which species are randomized on the phylogeny. Phylogenetic distance is calculated using the HKY clock model of evolution. Correlations are also found when CI and phylogenetic distances are calculated using the three other most parsimonious tree topologies and other models of evolution as well as when only the 12 most common species are used. Results of randomization tests for both co-occurrence and niche overlap based on basal area and presence/absence data matrices are shown in Table 4.
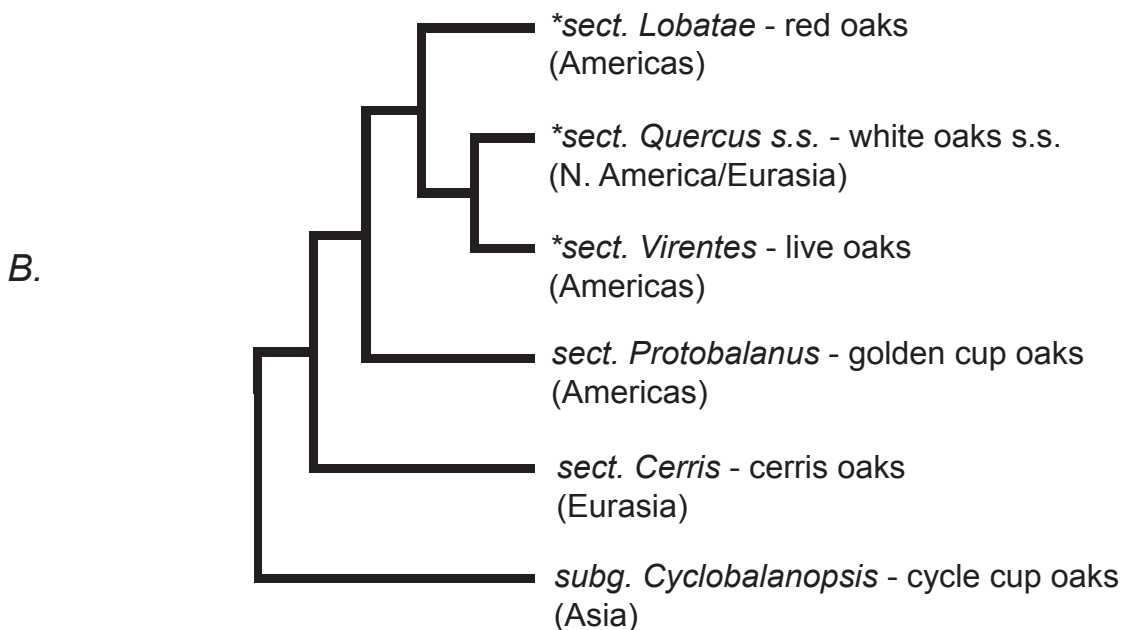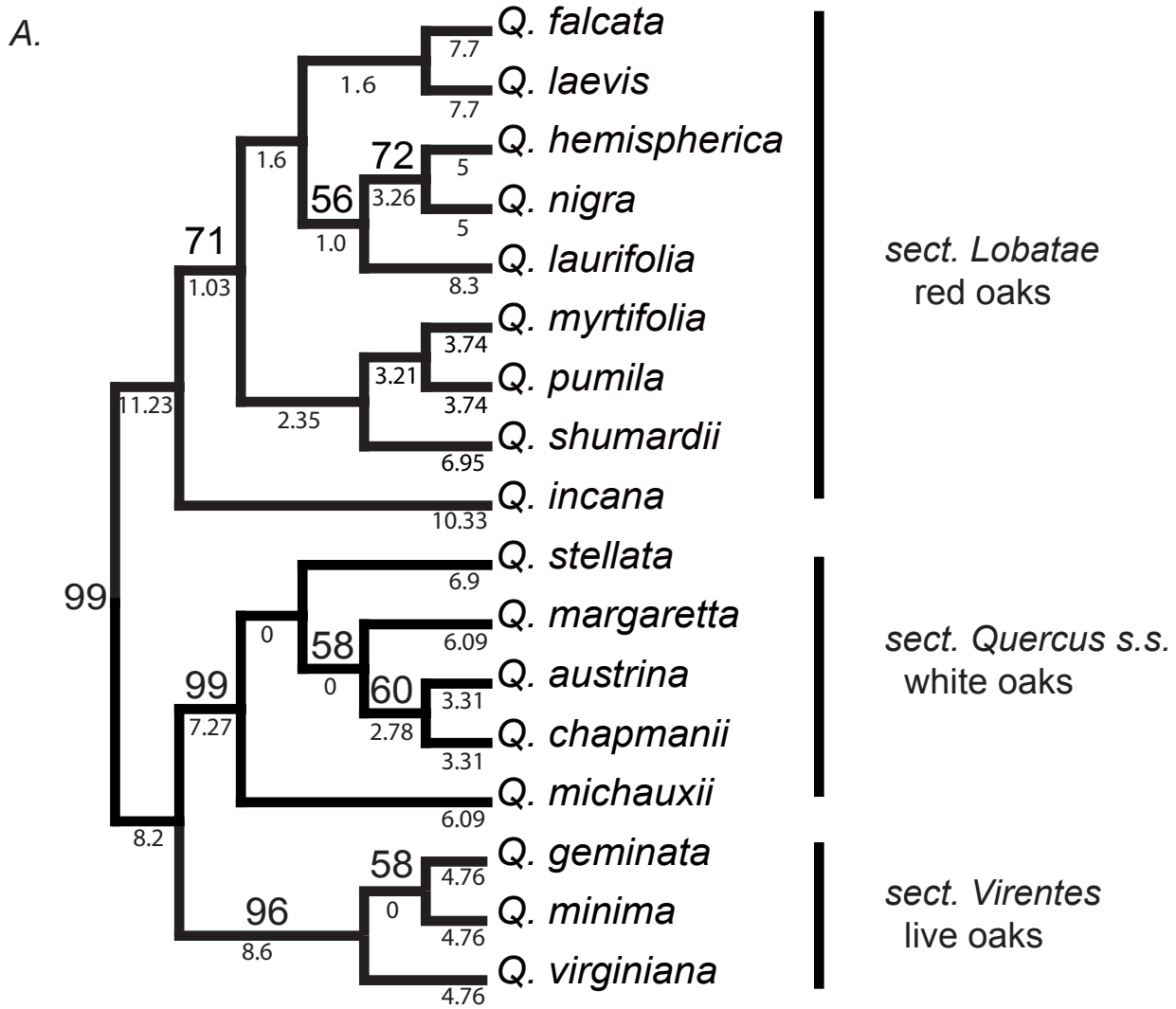
Figure 7
Proportion of total basal area is shown across seven levels of soil moisture, normalized by the number of plots per soil moisture level for the 8 species in the white+live oak clade (A) and for the nine species in the red oak clade (B). The collective distributions of the red oak clade and the white oak clade are shown in the bottom panel (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.
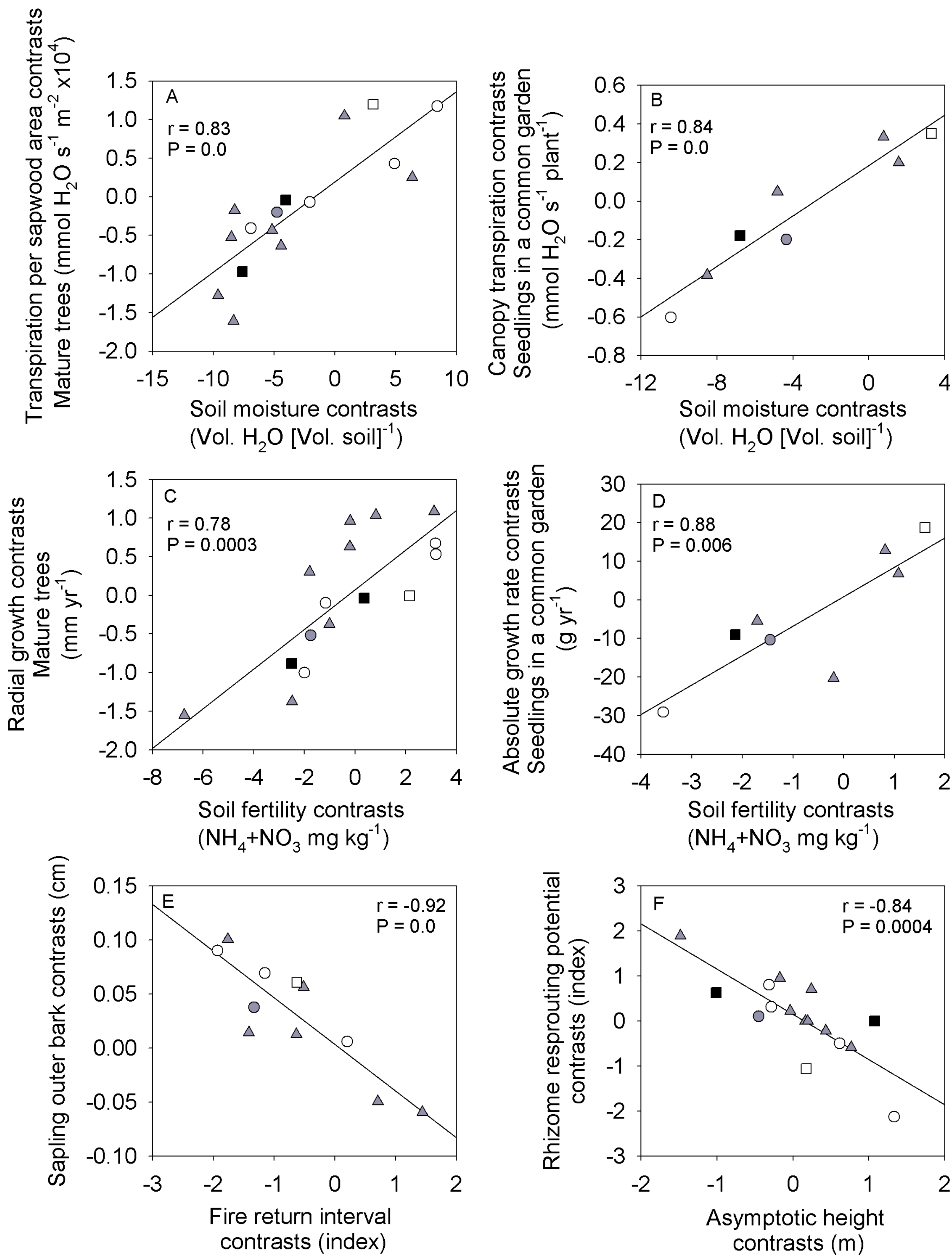
Fig. 1

	Data type	Abiotic Environment	Phenotypic Traits	Phylogenetic characters
Spatial Distribution	Presence/absence and basal area of species in random 0.10 ha plots	**Ordination/Detrended correspondence analysis (DCA)** Environmental factors influencing community structure	**Trait differences vs. Co-occurrence** Phenotypic attraction/repulsion (null models 2,3)	**Co-occurrence vs. phylogenetic distances** Phylogenetic attraction or repulsion (null model 1) **Niche overlap at different phylogenetic nodes** Phylogenetic depth of niche differentiation (null models 2,3)
Abiotic Environment	Soil moisture Soil fertility Fire regime (inferred)		**Independent Contrasts** ecological filtering/adaptation **Trait differences vs. niche overlap** Phenotypic attraction/repulsion (null models 2,3)	**Habitat divergence vs. phylogenetic distance** Habitat convergence or conservatism (null model 1)
Phenotypic Traits	Leaf-level traits and whole plant traits on mature trees in the field and on seedlings in a common environment			**Trait differences vs. phylogenetic distances** Trait convergence or conservatism (null model 1)
Phylogenetic Characters	ITS sequences			

Null models:
1) tip species randomized across phylogeny
2) Pres/abs - occurrences randomized across plots; species totals and plot totals constrained
3) Basal area randomized across pots for each species; species totals constrained

Fig. 3

A.

sect. *Lobatae* red oaks

Q. *falcata* 7.7
Q. *laevis* 7.7
Q. *hemispherica* 5
Q. *nigra* 5
Q. *laurifolia* 8.3
Q. *myrtifolia* 3.74
Q. *pumila* 3.74
Q. *shumardii* 6.95
Q. *incana* 10.33

sect. *Quercus s.s.* white oaks

Q. *stellata* 6.9
Q. *margaretta* 6.09
Q. *austrina* 3.31
Q. *chapmanii* 3.31
Q. *michauxii* 6.09

sect. *Virentes* live oaks

Q. *geminata* 4.76
Q. *minima* 4.76
Q. *virginiana* 4.76

B.

sect. Lobatae - red oaks (Americas)

sect. Quercus s.s. - white oaks s.s. (N. America/Eurasia)

sect. Virentes - live oaks (Americas)

sect. *Protobalanus* - golden cup oaks (Americas)

sect. *Cerris* - cerris oaks (Eurasia)

subg. *Cyclobalanopsis* - cycle cup oaks (Asia)

Source: Manos et al. (1999), Manos et al. (2001), Manos and Stanford (2001)

Fig. 4

Fig. 5 (Print in Black and White)

Soil moisture
Vol. H$_2$O / Vol. soil

6.1-8.3
8.3-10.5
10.5-12.7
12.7-14.8
14.8-17.0
17.0-19.2
19.2-21.4
21.4-23.6
23.6-25.8
25.8-28.0

Fig. 6

Co-occurrence
v. Phylogenetic Distance

Fig. 7