MULTIPLE TRAIT ASSOCIATIONS IN RELATION TO HABITAT DIFFERENTIATION AMONG 17 FLORIDIAN OAK SPECIES

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Abstract. Differentiation of species distributions along environmental gradients and phenotypic specialization help explain the co-presence of 17 oak species that might otherwise be expected to competitively exclude one another. In an effort to understand the role of niche differentiation in the co-presence of these congeneric species in north-central Florida, we examined the community structure of oak-dominated forests in this region in relation to environmental variables and a suite of life history and physiological traits. Landscape distribution patterns of oaks and other woody species were determined from randomly established plots in three state parks. Soil moisture, nutrient availability, and fire regime were found to be critical factors influencing community structure, and the distribution of oak species was strongly correlated with these gradients. Detrended correspondence analysis of species' distributions supported the grouping of oak species into three major community types: (1) hammock, (2) sandhill, and (3) scrub. Principal components of multiple traits also supported differentiation of oak species into these three groups.

There is clear evidence for ecological sorting among the oaks in these forests as species partition environmental gradients more than expected by chance, and most functional traits of species correspond to species distributions as predicted based on a priori understanding of trait function. Across phylogenetic lineages, species showed evolutionary convergence in function and habitat preference. In contrast, leaf-level traits were conserved within phylogenetic lineages and were not well correlated with local habitat factors, but rather with the broader geographic distributions and northern range limits of species. The cumulative results reported here provide strong evidence that oak species specialize for particular niches via trade-offs in functional traits, and such niche partitioning contributes to the high diversity of oak species at the landscape level. At smaller spatial scales, phylogenetic diversity among the oaks is likely to be important in promoting their coexistence through other mechanisms.

Key words: detrended correspondence analysis; fire regime; functional traits; leaf life span; phylogenetic lineage; Quercus; soil moisture; soil nutrients.

INTRODUCTION

A critical issue in ecology is understanding the forces that maintain biological diversity, both taxonomic and functional. Central to this question has been a quest to explain the patterns of species distributions and abundance across the landscape (Huston 1994) and to determine whether species specialize to partition the environment or whether distributions are the result of predominantly stochastic processes (Diamond and Case 1986, Brokaw and Busing 2000, Hubbell 2001). Although a number of mechanisms, including density-dependent mortality, are important in regulating relative abundance and diversity of species in both tropical (Wills et al. 1997, Wright 2002) and temperate systems (HilleRisLambers et al. 2002), such mechanisms do not explain the association of functional traits with habitat and resource regimes as niche theory does (McKane et al. 2002). Indeed, a central goal of many ecological studies has been to explain patterns of species distributions in relation to life history and functional traits (Monk 1966, Chabot and Hicks 1982, Hollinger 1992, Mulkey and Kitajima 1995, Reich et al. 1999, Ackerly et al. 2002).

North Central Florida is at the confluence of the northern temperate flora and the southern subtropical flora, providing a rich regional pool of species. Seventeen species of oaks are dominant or codominant with pines in forest communities across the landscape. Due to the potential for close relatives to competitively exclude one another, the coexistence of multiple congeners in this region is challenging to explain, particularly given the lack of major elevational gradients that occur in other regions of high oak diversity (Whittaker...
TABLE 1. A list of oak species in the study.

<table>
<thead>
<tr>
<th>Species Code</th>
<th>Species Name</th>
<th>General Habitat Type</th>
<th>Fire Frequency Ranking</th>
<th>Canopy Habit</th>
</tr>
</thead>
<tbody>
<tr>
<td>FA</td>
<td>Q. falcata</td>
<td>sandhill/hammock</td>
<td>2</td>
<td>deciduous</td>
</tr>
<tr>
<td>HE</td>
<td>Q. hemispherica</td>
<td>hammock</td>
<td>3</td>
<td>evergreen</td>
</tr>
<tr>
<td>IN</td>
<td>Q. incana</td>
<td>sandhill</td>
<td>1</td>
<td>brevideciduous</td>
</tr>
<tr>
<td>LV</td>
<td>Q. laevis</td>
<td>sandhill</td>
<td>1</td>
<td>deciduous</td>
</tr>
<tr>
<td>LA</td>
<td>Q. laurifica</td>
<td>hammock</td>
<td>5</td>
<td>brevideciduous</td>
</tr>
<tr>
<td>MY</td>
<td>Q. myrtifolia</td>
<td>scrub</td>
<td>evergreen</td>
<td></td>
</tr>
<tr>
<td>NI</td>
<td>Q. nigra L.</td>
<td>hammock</td>
<td>5</td>
<td>brevideciduous</td>
</tr>
<tr>
<td>PM</td>
<td>Q. pumila</td>
<td>scrub</td>
<td>evergreen</td>
<td></td>
</tr>
<tr>
<td>SH</td>
<td>Q. shumardii</td>
<td>hammock</td>
<td>4</td>
<td>deciduous</td>
</tr>
<tr>
<td>AU</td>
<td>Q. austrina</td>
<td>white hammock</td>
<td>3</td>
<td>deciduous</td>
</tr>
<tr>
<td>CH</td>
<td>Q. chapmanni</td>
<td>white scrub</td>
<td>brevideciduous</td>
<td></td>
</tr>
<tr>
<td>MA</td>
<td>Q. margaretta</td>
<td>white sandhill</td>
<td>1</td>
<td>deciduous</td>
</tr>
<tr>
<td>MX</td>
<td>Q. michauxii</td>
<td>white hammock</td>
<td>5</td>
<td>deciduous</td>
</tr>
<tr>
<td>ST</td>
<td>Q. stellata</td>
<td>white hammock</td>
<td>2</td>
<td>deciduous</td>
</tr>
<tr>
<td>GE</td>
<td>Q. geminata</td>
<td>live scrub</td>
<td>evergreen</td>
<td></td>
</tr>
<tr>
<td>MN</td>
<td>Q. minima</td>
<td>live scrub</td>
<td>evergreen</td>
<td></td>
</tr>
<tr>
<td>VI</td>
<td>Q. virginiana</td>
<td>live hammock</td>
<td>5</td>
<td>evergreen</td>
</tr>
</tbody>
</table>

Notes: Authorities are shown to the right of the species, along with a two-letter code and the major lineage to which it belongs. General habitat type, fire-frequency ranking (Jackson et al. 1999), and canopy habit are given. Definitions of general habitat type are as follows: sandhill = high pineland, open woodland, deep sands, high fire frequency (1–15 yr) with low severity; scrub = dense thicket, sandy soil, infrequent fire (15–50 yr) with high severity; hammock = mesic or hydric temperate hardwood forests with low or unpredictable fire frequency. Habitat descriptions are from Myers (1990), Platt and Schwartz (1990), and Kurz and Godfrey (1962).

- Soils underlain by limestone.
- Often found on limestone bluffs.
- Scrub soils frequently underlain by clay or marl.
- Seepage areas of sandy-clay upland; restricted to sites subject to burning.

1956, Platt and Schwartz 1990). One possibility is that oaks specialize into different niches, thus allowing them to partition the landscape and maintain their diversity. Here, we test the concept of the n-dimensional niche, (as defined by Bazzaz [1987], based on earlier conceptions of the niche by Hutchinson [1957] and Whittaker [1975]) using the distribution of oak species across critical environmental gradients. We refer to the physical gradients of the environment as habitat factors and the observed location of species across these gradients as habitats or realized niches.

While these oak species occur in close proximity, floristic studies have described them to be associated with distinct communities (hammock, sandhill, and scrub; Table 1), which vary markedly in soil water availability, fertility, and fire regime (Kurz and Godfrey 1962, Ewel 1990, Myers 1990, Long and Jones 1996). Oak species in this region also show significant variation in phenology and traits related to water use (Cavender-Bares et al. 1999, Cavender-Bares and Holbrook 2001), as found in other systems of high oak diversity (Knops and Koenig 1994, Villar-Salvador et al. 1997, Damesin et al. 1998).

The overarching impetus for the study was to understand factors that may help explain the maintenance of high oak diversity at the landscape level (1–100-ha scale) in north-central Florida. We first ask whether species are nonrandomly distributed across environmental gradients. This allows us to investigate whether distinct community affiliations of north Florida oaks described in the literature are supported by quantitative spatial analysis of species distributions relative to the abiotic environment. Second, if species are partitioning environmental gradients, what are the mechanisms, or functional traits, that allow them to do so? For example, do suites of leaf-level traits known to be associated with contrasting nutrient and water use strategies across a wide range of plant groups (e.g., Reich et al. 1997) allow oak species to specialize for particular resource regimes? In an effort to answer these questions, we sought to (1) quantify distributions of 17 sympatric oak species with respect to each other and other woody species; (2) analyze the distributions of species with respect to critical environmental factors; (3) determine whether species are partitioning their environment more than expected by chance using null models; and (4) determine whether and how functional traits of species correspond to their spatial distribution, their community affiliation, and to abiotic features of their habitats.

As a result of the typical geological features in north-central Florida, namely sand deposition on a clay layer or limestone bedrock, even minor topographic changes within a few meters of elevation cause marked changes...
in soil hydrology, and consequently nutrient availability and fire regime (Fig. 1) (Myers and Ewel 1990). In general, the wetter the site, the higher the productivity and nutrient availability and the lower the fire frequency. As fire frequency decreases, the fuel load and the fire intensity tend to increase (Jackson et al. 1999). However, in Florida, high temperatures combined with high humidity and soil moisture give rise to rapid decomposition; hence, fuel loading is not necessarily related to time since last fire, as in other systems. As a result, the more mesic and often lower elevation sites, dominated by hammocks of deciduous and evergreen broadleaf trees, are considered to have high productivity and high soil nutrient availability, as well as rare and unpredictable fire frequency (fire interval >100 yr with variable fire severity [Ewel 1990]). The higher elevation sites on thick sand deposits are xeric and infertile and, in the absence of fire suppression, are likely to harbor either sandhill or scrub communities. Although soil water and nutrient availability appear to vary little between sandhills dominated by longleaf pine (*Pinus palustris*) and scrub communities dominated by *Quercus* spp. or sand pine (*P. clausa*), they differ markedly in fire regimes (Myers 1985, 1990). The fire regime in scrub communities has been characterized as having a relatively frequent and predictable frequency (on the order of every 50 yr), but also as being quite severe with crown fires that destroy most of the aboveground biomass (Myers 1985, Myers 1990). The sandhill fire regime has been described as both frequent and predictable (1–15 yr) but consists largely of low-intensity surface fires that seldom extend into the crown (Myers 1990, Glitzenstein et al. 1995). These contrasting fire regimes are thought to be facilitated, at least in part, by the vegetation itself (Webber 1935, Menges and Hawkes 1998, Carrington 1999). Frequent fires in the sandhill communities are encouraged by grasses in the open understory and relatively flammable litter of longleaf pine in the sandhill communities while a dense layer of evergreen shrubs decreases fire frequency in scrub communities (Abrahamson and Hartnett 1990, Menges and Hawkes 1998). Unfortunately, precise records of fire frequency are lacking in most sites, but woody species composition of the community itself is considered as a good indicator of fire frequency and intensity (Jackson et al. 1999).

Based on theoretical considerations and prior empirical studies on the role of functional traits, we expected species occurring in communities prone to fire to have mechanisms of fire resistance (e.g., thick bark [Vines 1968, Jackson et al. 1999]) or post-fire recovery (e.g., clonal spreading and rhizome resprouting [Menges and Kohfeldt 1995, Carrington 1999]), and species’ traits related to growth and competitive ability to be positively correlated with soil resource availability (Tilman 1984, 1988, Goldberg 1997). Differences in stature, wood density, and seed size were also analyzed as important aspects of life history strategies that influence species distributions in other systems (Westoby et al. 1992, Baker et al. 2003, Meinzer 2003, Reich et al. 2003). Based on previous studies linking leaf longevity and specific leaf area to nutrient availability (Monk et al. 1989, Kikuzawa 1995, Reich et al. 1997, 1999, Givnish 2002) or water availability (Wright et al. 2001, Westoby et al. 2002), we expected leaf level
traits, including leaf life span and period of canopy foliation, to be negatively correlated with soil fertility, and we expected specific leaf area to be positively correlated with soil moisture and soil fertility. We also examined interspecific variation in species traits with respect to both community affiliation and phylogenetic lineage to determine whether traits tend to show similarity within communities, within lineages or both.

The combination of quantitative data on spatial distribution and community structure, species’ distributions with respect to environmental factors, and species’ functional traits both in situ and in a common garden provide us with a rare opportunity to examine whether niche differentiation is an important factor maintaining diversity among oaks of North Central Florida.

**METHODS**

Quantification of species spatial associations and environmental distributions

**Study sites and field sampling.**—Quantitative data on vegetation and soil variables were collected from randomly established 0.10-ha plots in three state parks in north-central Florida. The parks included San Felasco Hammock State Preserve, a 2803-ha park in Alachua County with major sinkhole formations including Sanchez Prairie and Church Swamp (31 plots); Ichetucknee Spring State Park, a 921-ha park bridging Columbia and Suwanee counties and bisected by the Ichetucknee river (20 plots); and Manatee Springs State Park, a 960-ha park abutting the Suwanee River in Levy County (21 plots). Parks were chosen that have had minimal disturbance in the last century, including large tracts of old growth, and in which attempts have been made to restore the fire regimes. Random plots were established in each park by dropping pine needles on a topographic map and marking where the tips fell. We then located the approximate coordinates of the marks on the ground and recorded UTM (Universal Transverse Mercator) coordinates using a hand-held GPS instrument (GPS 12, Garmin International, Inc., Olathe, Kansas, USA). Roads and park boundaries were excluded, as was the northern recent addition of San Felasco, which has experienced recent logging and agricultural disturbance. Two additional plots were established at Payne’s Prairie State Preserve and Morning Side Nature Center in Alachua County to increase the sampling of less common scrub species. Seventy-four plots were established in total. Based on visual inspection of their physiognomies, 48 plots were in hammock, 18 plots were in sandhill, and 8 plots were in scrub communities.

At each location, 20 × 50 m plots were established in an arbitrary orientation following the North Carolina Vegetation Survey Protocol (Peet et al. 1996). Within each plot, the dbh of each oak tree over 1.3 m height was measured for calculation of basal area and the species recorded. The presence/absence of other woody species was also recorded for each of the plots (Appendix A).

**Detrended correspondence analysis of species distributions.**—We used detrended correspondence analysis (DCA), an indirect method of gradient analysis, to compute ordinations of plots and species using (1) presence/absence data for all woody species, including oaks; (2) presence/absence of oaks only; and (3) relative basal area of oaks only. DCA was performed using the method of Hill (1979) with the DECORANA option in PC-ORD (McCune and Mefford 1997). We specifically used indirect gradient analysis because we wanted to describe community structure and examine species associations independently of environmental variables before we determined whether environmental variables were correlated with the community structure. Despite known limitations to DCA (e.g., Minchin 1987), it is generally the most widely used and cited ordination technique in the ecological literature and has advantages for our application in that plots and species are ordinated simultaneously.

We then tested whether values for soil variables, measured within each plot (see Soil nutrient and moisture measurements), were correlated with the plots scores from the vegetation data for the first two axes of ordination. We also tested whether species traits, including fire frequency classification (see Species niche overlap), were correlated with species scores on the first two axes of ordination.

**Soil nutrient and moisture measurements.**—Soil cores were collected in December 1998 from the top 10 cm of the soil, excluding undecomposed litter, in four subplots within each plot for a total of 296 individual samples. Subplot samples were used to calculate a plot mean for each soil variable after analysis. Soil samples were dried at 45°C for several days and passed through a 3-mm mesh sieve. Samples were analyzed for content of organic matter, calcium, nitrate N, ammonium N, labile phosphorus, potassium, and magnesium, as well as pH, at the soil testing laboratory of the University of Florida. Dried soil samples were extracted with Mehlich I extractant (0.05 moles/L HCl and 0.05 moles/L H2SO4) and the filtrate analyzed by inductively coupled argon plasma (ICAP) spectroscopy. Organic matter content, reported as a percentage of total weight, was analyzed by a modified Walkley-Black dichromate procedure for samples below 5% organic matter or by loss on ignition for samples above 5% organic matter. Nitrate N and ammonium N were extracted with KCl and analyzed colorimetrically with a lower detection limit of 0.2 μg/g. Ca, P, NH4-N and NO3-N are reported in units of mg/kg of soil.

Resin bags were also used to determine relative concentrations of exchangeable phosphorus. These were made from nylon hose filled with 14 g of anion and cation exchange resins (Iionac R NM-60, Sybron Chemicals, Inc., Birmingham, New Jersey, USA) and sealed with hot glue. They were initially soaked in 2 moles/L
KCl solution, rinsed with distilled water, and air dried following procedures adapted from Binkley and Matson (1983). Bags were inserted into the soil in four subplots within each plot to a depth of 5 cm in June 1999 within 2 to 3 d during which no rainfall events occurred. They were tied to markers with fishing line so that they could be easily retrieved. Bags were left in the ground for three months and removed at the end of summer within a 2–3-d period during which there was no precipitation. Resins were extracted with 2 moles/L KCl and filtrate was measured for P colorimetrically, reported in units of mg/kg of resin beads.

Soil water content integrated over 1 m depth was measured within four subplots of each plot using time domain reflectometry (TDR) and calibrated for two soil types (sandy soil with <5% organic matter and sandy soil with >5% organic matter). Five sets of measurements taken during all seasons over a 14-mo period between June 1998 and August 1999 were averaged for each plot. Calibration of the TDR measurements is described in Cavender-Bares and Holbrook (2001). Average plot values of soil moisture and nutrients were analyzed in relation to plot scores from the ordination analysis.

One limitation of our study is that, for practical reasons, we measured soil water content rather than soil water potential, which is more relevant to the physiological function of plants than soil water content. Due to the variation of soil moisture release curves not only across soil types, but also with soil depth, we did not have a reliable way to convert soil moisture to soil water potential. However, when we did estimate soil water potential using soil moisture release curves for Arredondo Fine Sand (Carlisle et al. 1988), the most appropriate match for most plots, it did not significantly change the results. Using soil water potential changes the shapes of the distributions across the water gradient, with higher resolution at drier sites and lower resolution at wetter sites. Nevertheless, the relative order of species along the spectrum from xeric to hydric soils does not change. The shapes of the relationships between species traits and the soil moisture regime also change depending on whether soil moisture or water potential is used. However, the association of traits with soil water regime is clear in either case. Hence, none of the major conclusions reached in the study are altered by this limitation.

Species niche overlap.—Pianka’s species overlap index (Pianka 1973) was computed for all pairwise combinations of oak species across seven resource levels for each of six soil factors. Overlaps were calculated based on relative basal area of species within plots using the following equation:

$$O_{jk} = O_{kj} = \frac{\sum_{i} E_{ij} F_{ik}}{\sqrt{\sum_{j} (E_{jk}) \sum_{i} (E_{ki})}}$$

where $O_{jk}$ is the overlap of species $j$ on species $k$. $i$ is the resource level, $n$ is the number of resource levels ($n = 7$), and $E_{ij}$ is the proportion of basal area of species $j$ in resource level $i$ divided by the number of plots that fall within resource level $i$ (Lawlor 1980). Bin width and number can influence the outcome of such analyses. We chose the smallest number of bins that gave good resolution of species niche structure while minimizing the number of empty bins. A sensitivity analysis showed that results were robust to bin width and that whether first and last bins were open or closed did not matter. Overlap values of species pairs were tested against a null model in which we randomized the raw data matrix by shuffling plot level values of relative basal area across plots. Each randomization procedure was run 1000 times and the significance of observed mean overlaps was tested against the distribution of the 1000 means of the random communities, as described above. This procedure was carried out by a program written in Visual Basic following methods similar to those described by Gotelli and Graves (1996), but it allowed us to randomize the raw data matrix rather than the derived values of proportion of basal area per resource level.

Testing for diversity–resource availability relationships.—The number of woody species and number of oak species per 0.10-ha plot were compared to mean soil fertility (nitrate N plus ammonium N) within plots to determine whether diversity was related to soil fertility. Plots were rank ordered by their soil fertility and divided into seven consecutive groups of 10 plots. The number of woody species, the number of oak species and the soil fertility was then averaged for each of the groups of plots.

Species, habitat preferences, range limits, and phenotypic traits

Species classification.—One issue that arises when studying promiscuous species, such as the oaks, is whether species are actually distinct entities. In this study region, species are phenotypically distinct (Kurz and Godfrey 1962), despite the tendency within the genus for introgression to occur. In a separate study, genetic data showed little relevant intraspecific variation and species monophyly was not strongly contradicted (Cavender-Bares et al. 2004), in contrast to previous studies in other regions (e.g., Whittemore and Schaal 1991). In southern latitudes where the growing season is long, including north-central Florida, temporal separation in flowering is thought to be an important prezygotic isolating mechanism preventing hybridization (Nixon 1985, 1997). Farther north, as the length of the growing season is reduced, such isolating mechanisms may no longer be possible and hybridization events may increase in frequency, reducing the distinctiveness of species. In this study region, however, oak species appear to adhere well to the ecological species concept (VanValen 1976, Mishler and Donoghue 1982, Daghlian and Crepet 1983) and are treated...
as distinct entities, following the taxonomic treatment of Kurz and Godfrey (1962).

*Species habitat preferences.*—We calculated species habitat preferences for several soil resources as the mean weighted soil moisture or nutrient value for each species according to the following equation:

\[
\mu^* = \frac{y_1x_1 + y_2x_2 + \cdots + y_nx_n}{y_1 + y_2 + \cdots + y_n}
\]

where \(\mu^*\) is the habitat preference (weighted mean); \(y_1, y_2, \ldots y_n\) are the basal area of the species within plots 1, 2, \ldots n; and \(x_1, x_2, \ldots x_n\) are the mean values of the environmental variable within plots 1, 2, \ldots n (ter Braak and Looman 1995).

*Fire frequency classification.*—Species were classified into categories of increasing fire frequency based on predictive models developed by Jackson et al. (1999) that link the following habitat types to fire regimes (see Table 1): (1) frequently flooded bottomland forest, (2) infrequently flooded bottomland forest, (3) moist upland forest, (4) intermediate dry, (5) dry upland forest, and (6) park-like forest/savanna (sandhill). Species were placed in these categories and assigned the corresponding rank. No rank was given to the five scrub species: *Quercus chapmanti*, *Q. pumila*, *Q. minima*, *Q. myrtifolia*, and *Q. geminata*.

*Geographic distributions of species.*—Northern range limits of species were determined from distribution maps from Nixon (1997) and Burns and Honkala (1990), as described in Cavender-Bares and Holbrook (2001). Temperature and season length covary with latitude and range limit can effectively serve as a proxy for season length.

*Physiological and morphological measurements of leaves of mature trees.*—Measurement of several leaf traits were carried out on six to 10 individuals of each species at San Felasco Hammock State Preserve or Payne’s Prairie State Preserve. Traits measured include gas exchange rates (leaf area and mass basis), laminar leaf area, specific leaf area, leaf nitrogen, and leaf chlorophyll content (data shown in Appendix B). All measurements were carried out on leaves of sun branches in order to control for light level, which has been shown to affect leaf life span and related leaf traits significantly (Williams et al. 1989, Reich et al. 1991, Ackerly 1996). Canopies of trees too tall to reach were accessed with the use of aerial lifts or scaffolding towers. Five such towers were erected in steep ravine areas not accessible with an aerial lift, allowing canopies of 15 trees to be reached in this manner. All measurements of gas exchange, SLA, total leaf N percent, and chlorophyll content were made during June on leaves of the first flush of the season. Carbon assimilation, stomatal conductance, and transpiration were measured with a portable gas exchange system (LI-6400, Li-Cor, Inc., Lincoln, Nebraska, USA) under saturating light (2000 \(\mu\text{mol-m}^{-2}\text{s}^{-1}\)) using the red–blue LED attachment of the LI-6400. Leaf temperature was controlled at 30°C. All gas exchange measurements were conducted in the morning between 08:00 and 11:00 hours on clear days in an effort to avoid stomatal depression with declining leaf water potential following methods of Cavender-Bares and Bazzaz (2000). Five leaves of each individual were measured. The leaves were removed for measurement of laminar leaf area (leaf size), determined by measuring fresh leaf area with the petiole removed using a LI-3000 portable leaf area machine (Li-Cor, Inc., Lincoln, Nebraska, USA). Leaves were oven dried for one week at 65°C and weighed to calculate specific leaf area (SLA; cm\(^2\)/g) and photosynthesis on a mass basis (\(A_{\text{max}}\)). Percent total leaf nitrogen (%N) was determined for three leaves of each tree measured. Dried leaf tissue was ground, and \(-200 \mu\text{g}\) was used to determine %N using a Europa Elemental Analyzer (model ANCA-sl) attached to a Europa model 20–20 Stable Isotope Analyzer via a capillary interface (Europa Instruments, Crewe, UK).

Relative chlorophyll content of leaves was measured with a SPAD-502 chlorophyll meter (Minolta, Tokyo, Japan) on leaves at the time of leaf removal from the tree. A previous study of chlorophyll in oak leaves found a linear relationship between relative SPAD units and chlorophyll content on an area basis within the range of values found in the current study. SPAD units were converted to chlorophyll content following methods described in Cavender-Bares et al. (2000) using the following equation:

\[
y = 5.53x - 62.9
\]

where \(y = \text{chlorophyll content (mg/m}^2\) and \(x = \text{SPAD absorbance (relative)}.\)

*Leaf life span and period of canopy foliation.*—Leaf life span—the number of days a leaf survives—was calculated for six to 10 mature trees of each species from leaf birth and death dates monitored on three branches per tree. Only four, three, and three individuals were measured for *Q. shumardii*, *Q. laurifolia*, and *Q. stellata*, respectively, because of the difficulty in accessing their canopies. Prior to leaf emergence, branches were flagged. After flushing occurred, the leaves were numbered with permanent ink on the tip of the leaf, and the birth date of each leaf was recorded. Each branch and each flush on each branch was color coded so that leaves could be counted with a spotting scope from the ground. Monthly surveys were conducted for a 14-mo period to determine the timing of new flushing events, to record the number of new leaves produced and record the numbers of leaves still present from each flush. By subtracting the number of remaining leaves from the number of leaves originally marked, survival time for each cohort of leaves was determined and recorded. The monthly surveys provided a 15-d resolution for each measurement. Every several months, new flushes were flagged and new leaves numbered. Flushing and leaf-fall dates were also monitored.
over a second year, and were similar to the first year; hence, only data from the first year are reported. We used two measures of leaf life span: (1) the mean leaf life span of the first cohort of leaves flushing in spring and (2) leaf life span averaged across all leaf cohorts. Species means for these two methods were highly correlated ($r = 0.89$). However, the first method was more consistent between the two years because it was less dependent on the timing of the onset of cold weather. Subsequent flushes tended to get truncated by chilling events, skewing the average. The first method is also better correlated with seedling leaf life span measured in a common environment without a cold period ($r^2 = 0.92$ vs. $r^2 = 0.85$). All analyses were done with both measures, and the results were very similar. For brevity, we report only the first method.

Period of canopy foliation was averaged for six to 10 individuals per species over a 2-yr period based on monthly surveys. The period of canopy foliation was calculated as the number of days per year that a tree maintained 50% or greater of its foliage relative to maximum summer foliage. Canopy habit was defined by period of canopy foliation as follows: deciduous $< 300 \text{d}$; brevifolious $\geq 300 \text{d}$ and $< 365 \text{d}$; evergreen $= 365 \text{d}$ (Table 1).

**Whole-plant traits of mature trees.**—Whole-plant traits, including asymptotic height, sapling outer bark thickness, maximum hydraulic conductance normalized by sapwood area (maximum $K_s$), whole-shoot transpiration normalized by sapwood area, Huber value (ratio of sapwood area to supported leaf area), native percent loss of conductivity (PLC, native embolism), wood density, radial growth rate, rhizome resprouting potential, and seed mass, unless otherwise indicated, were measured for six to 10 mature trees across the range of their distributions at San Felasco or Payne’s Prairie. Data are shown in Table 1 and Appendix C. Methods for determining maximum $K_s$, whole shoot transpiration, Huber value, and native PLC are described in Cavender-Bares and Holbrook (2001).

**Seed size.**—Size of acorns was determined both by volume and mass. Volume was calculated from radius ($r$) and height ($h$) of the fresh acorn assuming an ellipsoid shape using the equation: $4/3\pi r^2(h/2)$. Acorns were dried at 70°C for 3 d and weighed with and without the seed coat. Weights were only recorded for undamaged acorns. A minimum of 30 acorns were weighed per species, although volume was measured for 30–100 acorns per species. For 480 acorns from 16 species, an empirical relationship was determined between acorn volume ($V$) and acorn mass with seed coat removed ($M$): $M = 0.6363V - 0.1213$, $R^2 = 0.97$. Using this equation, seed mass for *Q. stellata* was determined from data collected from the U.S. Forest Service (Burns and Honkala 1990). We report seed mass without the seed coat as we assume that it is the most critical measure of seed size (Bazzaz 1997).

**Asymptotic height and rhizome resprouting potential.**—Asymptotic tree 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). We found our data to be in accord with data from the U.S. Forest Service and other published sources (Burns and Honkala 1990, Nixon 1997, Greenberg and Simons 1999). We used height information from Nixon (1997) for *Q. minima* and *Q. pumila*. For rhizome resprouting potential and clonal spreading (RhResprPot), a rank was assigned to each species based on 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) resprouting from rhizomes possible but rare, (3) occasional vegetative reproduction from rhizomes and clonal spreading in small patches, (4) considerable sprouting from roots and underground runners almost always present, including clonal spreading and dome formation.

**Outer bark thickness.**—We adapted methods described by Jackson et al. (1999) and Adams and Jackson (1995) to measure outer bark (rhytidome) thickness of saplings. Log-log regression equations of outer bark thickness vs. stem diameter were used to estimate outer bark thickness at stem diameters representing approximately one-quarter of the asymptotic tree height, based on relationships between stem diameter and height. Outer bark thickness of the short-statured runner oaks, *Q. pumila* and *Q. minima*, was estimated at 2 cm stem diameter, which corresponds to a stem height that is close to their maximum. We collected data for ~20 individuals per species for *Q. myrtifolia*, *Q. hemispherica*, *Q. pumila*, *Q. nigra*, *Q. minima*, *Q. chapmanii*, *Q. austrina*, *Q. falcata*, *Q. laevis*, *Q. margaretta*, *Q. incana*, and *Q. geminata*. Data for remaining species was taken from Jackson et al. (1999).

**Radial growth increment.**—Radial growth increment (mm/yr), a measure of absolute growth rate, was calculated from tree ring widths from tree cores of mature trees for 17 species. Cores were taken only from trees with straight trunks and fully exposed canopies. Cores were sanded until polished and viewed under a dissecting scope (Wild M3Z, Heerbrugg, Switzerland). Tree rings were measured to the nearest 0.01 mm using a Velmet Unislide tree ring measuring system (Velmet Company, New York, New York, USA) and software designed specifically for collecting tree ring data (Measure J2X version 2.2.6, Voortech Consulting, Holdenness, New Jersey, USA; tree ring data bank). Annual growth increments vary with stem diameter, age, life history stage and growth conditions (Clark and Clark

1999). Moreover, stem diameters and age at maturity vary greatly among these oak species, making comparison of growth rates difficult. In an effort to account for these factors, we averaged 10 consecutive growth increments for each individual during its maximum growth phase after reaching reproductive age. Reproductive ages for each species were based on data from Burns and Honkala (1990) and Kurz and Godfrey (1962). For the runner oaks (Q. pumila and Q. minima), which are reproductive after only a few years, the last five annual growth increments were used.

Wood density.—Density of sapwood was determined from tree cores or small segments for six to 10 individuals of the same species as explained for radial growth. Volume was determined for fresh samples from radius and length measurements of the cores or by volume displacement in distilled water. Dry wood mass was determined by weighing oven-dried samples.

Seedling traits from a glasshouse experiment

Because species differences in phenotypes expressed in their native habitats reflect both genetic and environmental differences, in situ field measurements of individuals alone do not allow clear assessment of evolutionary divergence. Therefore, it is important to examine the association of species traits expressed under common garden conditions with habitat preferences determined in the field. Hence, in addition to leaf and whole-plant traits of adult trees in situ, seedling traits were determined in a glasshouse for a subset of species included in the analysis.

Growth conditions.—Plants were grown in glasshouse facilities at Harvard University. Acorns were collected in the fall of 1996 in north-central Florida for the nine species: Q. falcata, Q. geminata, Q. hemisphérica, Q. laevis, Q. margaretta, Q. michauxii, Q. myrtifolia, Q. nigra, and Q. myrtifolia. Q. alba, considered a hammock species, whose range begins just north of the field study area, was also included in the common garden study although it was not represented in the field study. Acorns were stored in a cold room at 5°C after collection and planted in 60 × 35 × 20 cm tubs with Promix potting soil (Premier Horticulture, Dorval, Quebec, Canada) in the spring of 1997. Germination took ~1–2 mo. Germinants were transplanted into individual 12-L tree pots within 1–2 wk after emergence. The soil in these pots included a 2-cm layer of gravel and 2 cm of Turfus (Profile Products, Buffalo Grove, Illinois, USA) at the bottom of the pot. Pots were then filled to the surface with sand and a small amount of peat and field soil. At the time of transplanting, the date was recorded, and initial measurements were made on stem height, root and stem diameter, number of leaves, and length of the longest leaf. Approximately 40 plants were transplanted per species, depending on germination rates and viability of acorns. At least 30 additional plants per species were measured, dried, and weighed to determine allometric relationships between measured variables and biomass. Temperature was maintained at circa 28°C during the day and 20°C at night.

Seedling growth rates.—Absolute and relative growth rates were measured on all species in the experiment. Absolute growth rate (AGR, g/yr) was determined from dry biomass. Relative growth rate (RGR, g·g⁻¹·d⁻¹) was calculated as follows:

\[
RGR = \frac{\log(M_{\text{final}}) - \log(M_{\text{initial}})}{T_{\text{final}} - T_{\text{initial}}} \tag{1}
\]

where \(M_{\text{final}}\) and \(M_{\text{initial}}\) are biomass at the time of harvest \(T_{\text{final}}\) and the time of transplanting \(T_{\text{initial}}\) (Hunt 1982).

Allometric equations were developed relating plant parameters—including stem height, stem diameter, leaf number, and length of longest leaf—to dry biomass based on separate harvests of at least 30 seedlings per species (Appendix D). These equations were used to estimate \(M_{\text{initial}}\) from nondestructive measurements on the common garden plants.

Leaf-level traits.—Leaf life span was determined by recording birth and death dates of leaves from apical shoots on ~15 individuals per species. Leaves were surveyed weekly for a 16-mo period, providing high resolution for these data. Gas exchange was measured on 10–15 individuals per species in late July, controlling light level (1500 μmol·m⁻²·s⁻¹) using a LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). After photosynthesis was measured, a leaf disk of known area was removed in the same area on the leaf where gas exchange was measured. Large primary and secondary veins were avoided. The disk was weighed with a microbalance for calculation of \(A_{\text{max}}\). Leaf laminar area (leaf size), and specific leaf area (SLA) were measured for multiple leaves per individual at the time of harvest in the same manner as described for mature trees. Whole plant transpiration rates were calculated by multiplying mean maximum transpiration rates per species by the average leaf surface area per species.

Linking functional traits, habitat variables, and community affiliations

Independent contrast correlations.—Using hypotheses about phylogenetic relationships between species, determined in a separate study (Cavender-Bares et al. 2004), we examined the direction and magnitude of evolutionary change in particular traits in relation to other traits or habitat preferences, following the method originally proposed by Felsenstein (1985) and standardized by branch lengths (Garland et al. 1992). By reconstructing ancestral states of traits, this method allowed us to examine evolutionary trade-offs and patterns of correlated evolution among traits and habitat preferences. Analyses were carried out using four equally likely tree topologies in the program CACTUS (Schwikl and Ackerly 2001).7

7 (http://www.pricklysoft.net/software/caactus.html)
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Principal components analysis.—PCA for traits of mature trees and for traits of seedlings in the common garden were carried out using Data Desk v. 6.0 (Data Description, Inc., Ithaca, New York, USA) to determine whether functional traits of species group by the three community types—hammock, sandhill, and scrub. Traits included in the mature tree PCA were rhizome resprouting potential, wood density, Huber value, maximum leaf life span, radial growth rate, asymptotic height, seed mass, native PLC, maximum $K_s$, $A_{mass}$, laminar leaf area, whole-shoot transpiration, and SLA. Traits included in the seedling PCA were SLA, seed mass, laminar size, absolute growth rate, relative growth rate, whole plant transpiration, $A_{mass}$, and leaf life span.

Testing for species similarity within communities and lineages.—Multiple analysis of variance (MANOVA) was used to determine whether variation among species in (1) spatial distribution (axis scores from the DCA analyses) and (2) habitat preferences (weighted mean values of each soil factors for each species) could be explained either by the preassigned community affiliations, treated as a fixed effect with three levels, or by phylogenetic lineage, treated as a fixed effect with three levels. For the ordination data, first- and second-axes scores were included as dependent variables in the MANOVA, but separate tests were run for the two different DCA analyses. For habitat preferences, species mean, weighted values for soil moisture, soil pH, soil nitrate N plus ammonium N, soil calcium, and organic matter content were treated as dependent variables. We also used univariate ANOVAs to determine whether community affiliation or lineage explained interspecific variation in functional traits. All analyses were carried out in Data Desk v. 6.0.

RESULTS

Quantification of species distributions

Indirect gradient analyses.—The results of the ordination analyses based on presence/absence of all species (Fig. 2A), on presence/absence of oaks only, and on relative basal area of oaks (Fig. 2B) indicate that the community structure we observed is well described by the first and second axis of ordination. For brevity, the analysis of presence/absence of oaks only is not shown, but the results closely resemble the first analysis. The eigenvalues for the first axis ranged from 0.66 to 0.88 and from 0.42 to 0.53 for the second axis (Table 2). Both ordinations show clustering of species within each of the three community types. In the analysis using relative basal area of oaks, however, there is greater resolution in the spatial distribution of hammock species and less resolution in the distribution of scrub species relative to the presence/absence ordination.

Average plot values of soil moisture and all soil fertility factors, except soil pH, were significantly negatively correlated with the first axis of ordination in all three analyses (Table 2). Soil moisture and soil fertility parameters across plots covaried to a large extent (Table 3) and cannot be statistically separated. The highest covariance was found among the cations, Ca, Mg, and K. Fire frequency classification of tree species by Jackson et al. (1999) (Table 1) was also highly correlated with this axis (see also Table 6) indicating that fire frequency covaries inversely with soil moisture and resource availability. Soil moisture was the only environmental parameter significantly correlated with the second axis in the presence/absence analyses (Fig. 2A). In the analysis using relative basal area (Fig. 2B), the species are distributed somewhat differently across the two axes and the second axis is weakly correlated with

![Fig. 2. Scatter diagrams showing species scores in relation to the first and second axes after DCA using presence/absence for (A) all woody species within plots and (B) relative basal area of oak species. Phylogenetic lineages of each species are shown with symbols. Three distinct community types can be identified and are indicated with different shading (shown for oaks only): scrub, black; sandhill, gray; hammock, open symbols.](image-url)
scrub oak species, particularly *Q. chapmanii*, found in association with a high diversity of woody species. Proportion of total basal area per soil moisture overlap were found in association with species are not labeled, however, sandhill oak species and *Carya* spp., and *Liquidambar styraciflua* were found in association with *Q. geminata* and *Q. falcata*. For simplicity, the non-oak species or relative basal area of oaks within the 74 plots.

Species distributions across resource axes and niche overlap.—Proportion of total basal area per soil moisture level are shown in Fig. 3 for seven resource bins. The upper row shows sandhill species that are restricted to dry sites, particularly *Q. laevis* and *Q. margaretta*, which only occur in the driest resource level. *Q. incana* and *Q. falcata* occur in the first two driest resource levels, and *Q. falcata* also has a small presence in wetter sites. The second row shows scrub species, which also largely occur in dry sites, but are less restricted than sandhill species. *Q. minima* and *Q. pumila* (similar distribution as *Q. minima*, but not shown) actually occur in intermediate soil moisture regimes. *Q. geminata* shows its highest abundance at low soil moisture but still maintains a low presence even in the wettest soil moisture level. Hammock species, shown in the third and fourth rows, all occur in the wettest soils but many of them also occur in dry soils. Hammock species, in general, tend to have broader distributions across the soil moisture gradient than sandhill or scrub species.

Mean niche overlap of all species, based on Pianka’s niche overlap test, was significantly less than expected across gradients of soil moisture and pH (Table 4). Species pairwise overlap values for soil moisture are given in Appendix E. The same result was obtained if

### Table 2. Pearson and Kendall correlation coefficients (r) of soil parameters measured in 74 plots in relation to the first and second ordination axes based on presence or absence of all species or relative basal area of oaks within the 74 plots.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Presence/absence: all species</th>
<th>Relative basal area: oaks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Axis 1 (r)</td>
<td>Axis 2 (r)</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>-0.55</td>
<td>0.31</td>
</tr>
<tr>
<td>NH$_4$-N</td>
<td>-0.58</td>
<td>0.21</td>
</tr>
<tr>
<td>NO$_3$-N</td>
<td>-0.33</td>
<td>0.09</td>
</tr>
<tr>
<td>Organic matter</td>
<td>-0.47</td>
<td>0.27</td>
</tr>
<tr>
<td>P (soil samples)</td>
<td>-0.38</td>
<td>0.05</td>
</tr>
<tr>
<td>P (resin bags)</td>
<td>-0.38</td>
<td>0.16</td>
</tr>
<tr>
<td>Ca</td>
<td>-0.59</td>
<td>0.20</td>
</tr>
<tr>
<td>Mg</td>
<td>-0.57</td>
<td>0.18</td>
</tr>
<tr>
<td>K</td>
<td>-0.58</td>
<td>0.26</td>
</tr>
<tr>
<td>pH</td>
<td>-0.19</td>
<td>0.28</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>0.66</td>
<td>0.42</td>
</tr>
</tbody>
</table>

**Notes:** Eigenvalues are shown below the columns for each axis. Correlation coefficients >0.3 or <−0.3 are shown in boldface (df = 73).

### Table 3. Pearson correlation coefficients for relationships among soil parameters within plots (N = 74).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Soil moisture</th>
<th>OM</th>
<th>NO$_3$-N</th>
<th>NH$_4$-N</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>OM</td>
<td>0.50</td>
<td>0.29</td>
<td>0.51</td>
<td>0.51</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO$_3$-N</td>
<td>0.29</td>
<td>0.64</td>
<td>0.19</td>
<td>0.42</td>
<td>0.42</td>
<td>0.48</td>
<td>0.29</td>
<td>0.77</td>
</tr>
<tr>
<td>NH$_4$-N</td>
<td>0.51</td>
<td>0.51</td>
<td>0.29</td>
<td>0.74</td>
<td>0.63</td>
<td>0.77</td>
<td>0.48</td>
<td>0.53</td>
</tr>
<tr>
<td>P</td>
<td>0.54</td>
<td>0.58</td>
<td>0.45</td>
<td>0.59</td>
<td>0.82</td>
<td>0.77</td>
<td>0.31</td>
<td>0.66</td>
</tr>
<tr>
<td>K</td>
<td>0.50</td>
<td>0.67</td>
<td>0.77</td>
<td>0.67</td>
<td>0.67</td>
<td>0.78</td>
<td>0.53</td>
<td>0.41</td>
</tr>
<tr>
<td>Mg</td>
<td>0.50</td>
<td>0.00</td>
<td>0.14</td>
<td>0.31</td>
<td>0.20</td>
<td>0.29</td>
<td>0.31</td>
<td>0.66</td>
</tr>
<tr>
<td>Ca</td>
<td>0.50</td>
<td>0.50</td>
<td>0.77</td>
<td>0.67</td>
<td>0.78</td>
<td>0.41</td>
<td>0.77</td>
<td>0.66</td>
</tr>
</tbody>
</table>

**Notes:** Coefficients >0.30 are shown in boldface. The table indicates a high degree of covariance among soil fertility parameters and soil moisture. Organic matter is abbreviated as OM.
soil moisture data were converted to soil water potential based on soil moisture release curves for Arredondo Fine Sand (Carlisle et al. 1988) and divided into seven bins ($P < 0.001$; 1000 simulations > observed). A sensitivity analysis for soil moisture showed that the analyses were robust to changes in bin width and that a two-fold increase in the number of bins still gave rise to lower niche overlap than expected. Forty-eight out of 136 total species pairs showed less overlap than expected across the soil moisture gradient. Only 10 pairs showed more overlap than expected. Mean niche overlap of all species across all soil factors tested was significantly less than expected ($P < 0.001$, Table 4). Soil moisture is less important for niche partitioning among hammock species, examined by themselves ($P > 0.192$, Table 4), although hammock species are partitioning the pH gradient ($P < 0.002$). At the same time, calcium is more important for niche partitioning among hammock species ($P < 0.056$), than among all species ($P < 0.49$).

MANOVA results show that spatial distributions of species are highly significantly explained by preassigned community affiliations, but not by phylogenetic lineage. This result is the same whether DCA axes scores from the presence/absence analysis (Table 5) or from the relative basal area analysis are used (not shown). Species habitat preferences with respect to soil properties are also significantly explained by community affiliation but not by phylogenetic lineage (Table 5). Species habitat preferences for soil moisture, soil nitrate and ammonium, soil calcium, organic matter content, and pH differed among the communities, but not among lineages. Scheffe’s post hoc tests show the significant difference in species soil preferences among communities arises from differences between preferences of hammock and scrub species and between hammock and sandhill species, but not between sandhill and scrub species. The same result emerges if soil properties of scrub, hammock and sandhill plots are compared, rather than species habitat preferences.

**Functional traits of species in relation to community structure, habitat preferences, and phylogenetic lineage**

**Species traits in relation to ordination axes.**—Native embolism, radial growth rate, whole-shoot transpiration normalized by sapwood area, asymptotic height, seed mass, $A_{max}$, and maximum $K_s$ of mature trees were all significantly correlated with species scores for the first axis of ordination (Table 6). Seedling traits related
to gas exchange and growth, including absolute growth rate, whole plant transpiration, $A_{\text{max}}$, and RGR, were significantly correlated with the first axis of ordination. Fire-frequency classification of individual species (Table 1) was highly correlated with the first axis of ordination for all ordination analyses (correlation excludes scrub species shown in black). Both rhizome sprouting potential and sapling outer bark thickness were also correlated with the first axis of ordination, with hammock species having little rhizome resprouting potential relative to scrub species and sandhill species having greater bark protection than hammock and scrub species (Table 6, Fig. 4).

Period of canopy foliation for mature trees was correlated with the second axis of Fig. 2A: scrub species tend to be evergreen or brevideciduous while sandhill species are largely deciduous. Other leaf-level traits of mature trees, including laminar leaf area, chlorophyll content, $A_{\text{max}}$, SLA, period of canopy foliation, and mean or maximum leaf life span were not correlated with either of the DCA axes. $A_{\text{max}}$ is defined as the maximum CO$_2$ assimilation rate on a leaf-area basis, measured in the morning under saturating light at ambient temperature and 350 μL/L CO$_2$. Seedling leaf life span was also correlated with the second axis of ordination: the two scrub species in the seedling experiment (Q. myrtifolia and Q. geminata) had longer-lived leaves (both evergreen) than the sandhill hill species (Q. margaretta, Q. laevis, and Q. falcata), all deciduous. The brevideciduous scrub species, Q. pumila and Q. chapmani, which have intermediate leaf life spans, and the sandhill species (Q. incana), which has a short leaf life span (5.4 mo) were not included in the seedling study, which accounts for the significant correlation for seedling leaf life span but not leaf life span of mature trees.

### Table 5. MANOVA results testing whether communities or phylogenetic lineages, treated as main fixed effects, significantly explain the variance among groups of dependent variables: spatial distribution and habitat preferences.

<table>
<thead>
<tr>
<th>Main effect</th>
<th>Spatial distribution (DCA axis scores)$^*$</th>
<th>Habitat preferences (soil factors)$^\dagger$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylogenetic lineage§</td>
<td>Wilks’ lambda 0.888, P 0.807, df 4, 26</td>
<td>Wilks’ lambda 0.477, P 0.757, df 12, 18</td>
</tr>
<tr>
<td>Community¶</td>
<td>Wilks’ lambda 0.078, P 0.0001, df 6, 24</td>
<td>Wilks’ lambda 0.081, P 0.006, df 12, 18</td>
</tr>
</tbody>
</table>

$^*$ First and second axis scores for oak species from detrended correspondence analysis of occurrences of all woody species within random plots.

$^\dagger$ Species weighted mean values for soil moisture, organic matter content, exchangeable phosphorus, exchangeable nitrate and ammonium, pH, and calcium content.

§ Red, white, and live oaks.

¶ Sandhill, scrub, and hammock.
NH₄-N and mean soil moisture of species habitats. Both mature tree radial growth and seedling RGR showed a trend of asymptotically higher values with higher resource availability (Fig. 5E–H).

Traits known to be important in influencing water transport and loss in other systems, including wood density, hydraulic conductance, native embolism (PLC), and whole-shoot transpiration, were examined in relation to species soil moisture preferences using standard correlations and independent contrast correlations. Interestingly, using a standard correlation, wood density was not directly correlated with the soil moisture gradient (Fig. 6A) because the trait is conserved within lineages, and live oaks have much denser wood than other species. Independent contrasts, however, which allow trait conservatism within lineages to be factored out, showed a significant decrease in wood density with increasing soil moisture (Fig. 6B), consistent with findings in other systems (Meinzer 2003). Hydraulic conductance, native embolism (PLC), and whole-shoot transpiration were all significantly correlated with soil moisture preferences and showed significant patterns of correlated evolution with habitat preferences using independent contrasts (Fig. 6C–H).

These patterns give rise to very clear evolutionary trade-offs, for example, between maximum height and the ability of plants to resprout from rhizomes after fire (Fig. 7A) or the native embolism of the xylem and the hydraulic capacity of stems (Fig. 7C), providing support for a safety–efficiency trade-off (Sperry 1995, Hacke and Sperry 2001). At the same time, growth and height show a strong correspondence, as documented in other systems (Thomas 1996, Baker et al. 2003).

At the leaf level, $A_{\text{max}}$ and SLA were significantly correlated with foliar N concentration when examined

<table>
<thead>
<tr>
<th>Trait</th>
<th>Presence/absence: all species</th>
<th>Basal area: oaks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Axis 1 ($r$)</td>
<td>Axis 2 ($r$)</td>
</tr>
<tr>
<td>Mature trees: field</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fire-frequency ranking</td>
<td>-0.88</td>
<td>0.83</td>
</tr>
<tr>
<td>Sapling bark thickness</td>
<td>0.41</td>
<td>-0.78</td>
</tr>
<tr>
<td>Rhizome sprouting potential</td>
<td>0.76</td>
<td>0.25</td>
</tr>
<tr>
<td>PLC</td>
<td>-0.66</td>
<td>-0.17</td>
</tr>
<tr>
<td>Radial growth</td>
<td>-0.60</td>
<td>-0.14</td>
</tr>
<tr>
<td>Whole-shoot transpiration</td>
<td>-0.56</td>
<td>-0.08</td>
</tr>
<tr>
<td>Asymptotic height</td>
<td>-0.53</td>
<td>-0.43</td>
</tr>
<tr>
<td>Seed mass</td>
<td>-0.53</td>
<td>-0.23</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>-0.51</td>
<td>-0.48</td>
</tr>
<tr>
<td>Maximum $K_c$</td>
<td>-0.49</td>
<td>-0.07</td>
</tr>
<tr>
<td>Leaf size</td>
<td>-0.32</td>
<td>-0.39</td>
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<tr>
<td>Chlorophyll content</td>
<td>-0.26</td>
<td>0.22</td>
</tr>
<tr>
<td>SLA</td>
<td>-0.18</td>
<td>-0.19</td>
</tr>
<tr>
<td>Period of canopy foliation</td>
<td>0.05</td>
<td>0.49</td>
</tr>
<tr>
<td>Leaf life span</td>
<td>0.09</td>
<td>0.44</td>
</tr>
<tr>
<td>Wood density</td>
<td>0.12</td>
<td>0.47</td>
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<tr>
<td>Huber value</td>
<td>0.18</td>
<td>0.16</td>
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<tr>
<td>Seedlings: common garden</td>
<td></td>
<td></td>
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<tr>
<td>AGR</td>
<td>-0.87</td>
<td>0.14</td>
</tr>
<tr>
<td>Whole-plant transpiration</td>
<td>-0.77</td>
<td>0.02</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>-0.67</td>
<td>0.43</td>
</tr>
<tr>
<td>RGR</td>
<td>-0.65</td>
<td>0.39</td>
</tr>
<tr>
<td>SLA</td>
<td>-0.31</td>
<td>-0.28</td>
</tr>
<tr>
<td>LAR</td>
<td>-0.58</td>
<td>-0.60</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>-0.39</td>
<td>0.50</td>
</tr>
<tr>
<td>Leaf life span</td>
<td>0.05</td>
<td>0.73</td>
</tr>
<tr>
<td>Laminar leaf area</td>
<td>-0.54</td>
<td>-0.03</td>
</tr>
</tbody>
</table>

**Notes:** Correlation coefficients $\geq 0.48$ are shown in boldface. $N$ is the number of species for which data were available. For mature trees, units are as follows: maximum $K_c$ (maximum hydraulic conductance; kg H₂O·s⁻¹·m⁻¹·MPa⁻¹); transpiration per sapwood area (mmol H₂O·m⁻²·s⁻¹); chlorophyll content (relative units); radial growth increment (cm/yr); fire frequency ranking (excluding scrub species; taken from Jackson et al. [1999]); asymptotic height (m); rhizome resprouting potential (index); sapling bark thickness (mm); period of canopy foliation (d); wood density (g/m³); leaf life span (d); maximum assimilation rate ($A_{\text{max}}$; μmol CO₂·m⁻²·s⁻¹); maximum assimilation rate-mass basis ($A_{\text{max}}$; μmol CO₂·g⁻¹·s⁻¹); chlorophyll content (mg/m²); seed size (seed mass without the seed coat; g); leaf size (laminar leaf area; cm²); Huber value (ratio of sapwood area to leaf area); native percentage loss of conductivity (PLC). For seedlings, units are: absolute growth rate (AGR; g/yr); relative growth rate (RGR; g·g⁻¹·d⁻¹); whole-plant transpiration (mmol H₂O·m⁻²·s⁻¹); laminar leaf area (cm²); SLA (cm²/g); leaf life span (d); $A_{\text{max}}$ (μmol CO₂·m⁻²·s⁻¹); $A_{\text{max}}$ (μmol CO₂·g⁻¹·s⁻¹); leaf area ratio (LAR; m²/g).
on an individual leaf basis (Appendix F). These relationships varied across phylogenetic lineages, however, and were strongest within the live oak group. SLA was not significantly correlated with %N within the red oaks or white oaks. An overall correlation arises because live oaks have relatively low SLA and low %N while white oaks tend to have higher %N and higher SLA (Appendix F). There is high variation in the relationships among leaf traits within the red oaks. In particular, *Q. incana* behaves as an outlier species with relatively high $A_{max}$, high SLA, and short leaf life spans but low %N. Indeed, $A_{max}$ and %N are correlated within the red oaks only when *Q. incana* is removed from the analysis (Appendix F). At the species level, leaf traits including $A_{max}$ and leaf life span were only weakly correlated with foliar N concentration (Table 7). Other traits, however, including period of canopy foliation and SLA were more strongly correlated with leaf N. Yet, contrary to expectation, leaf-level traits were not correlated with soil fertility or soil moisture (Table 7). These results are the same regardless of which soil factors are examined and if independent contrast cor-
relations are used instead of standard correlations (data not shown). If sandhill species are removed, leaf life span and period of canopy foliation tend to decline with increasing soil fertility as expected, although the statistical power is limited with only 13 species, and these trends are not significant. In contrast, leaf-level traits, with the exception of SLA, correspond well to the northern range limit of the species geographic distributions (Table 7). Southern species have longer leaf life spans and shorter periods of canopy foliation than northern species. In addition, southern species have smaller leaves, lower $A_{\text{mass}}$, and lower N concentration than northern species.

**Adult traits measured in situ vs. seedling traits in a glasshouse**

The degree to which traits measured in the field reflect intrinsic properties of species rather than responses to the environment is not known. However, a substantial component of these traits appears to be intrinsic, given strong correlations between seedling traits measured in a common environment and mature traits measured in the field (Appendix G). Several of the traits measured on seedlings could be directly compared to the same traits or to similar kinds of traits as those measured on mature trees in the field (Appendix G). Radial growth rates of adult trees were correlated with relative growth rates of seedlings (RGR) measured under standardized favorable conditions in a glasshouse ($r = 0.66$; Appendix G). Seedling absolute growth rates were highly correlated with max. hydraulic conductance ($r = 0.823$) and with transpiration rates on a sapwood area basis of mature trees ($r = 0.86$). Physiological correlates of plant growth rates, e.g., transpiration rates, SLA, and $A_{\text{max}}$, were also correlated between adult trees and seedlings. Shoot-level transpiration rates (per unit sapwood area) of adult trees were also positively correlated with whole plant transpiration of seedlings ($r = 0.90$; Appendix G). SLA of seedlings and mature trees showed a strong correlation ($r = 0.81$; Appendix G), although seedlings had much higher SLA than mature trees. Laminar leaf area was also significantly correlated ($r = 0.76$) but seedlings had smaller leaves than mature trees. Light saturated
photosynthetic rates measured on a leaf area basis ($A_{\text{max}}$) in the common garden and in the field were strongly correlated ($r = 0.81$) although mature trees had higher photosynthetic rates than seedlings. $A_{\text{max}}$ was not correlated between seedlings and mature trees ($r = 0.41$). Thus, the significant correlation of $A_{\text{max}}$ between adult and seedlings was largely due to SLA. Seedling leaf life span was very highly correlated with leaf life span of mature trees ($r = 0.92$). The relationship was very close to the 1:1 line, but seedling leaf
Fig. 7. Independent contrast correlations of species traits showing evolutionary trade-offs and correlations: (A) contrasts in rhizome resprouting potential in relation to contrasts in asymptotic height; (B) contrasts in radial growth in relation to height; (C) contrasts in percentage loss of hydraulic conductivity in relation to maximum hydraulic conductivity. R values for the plotted contrasts are given along with a range of P values for contrasts using four equally likely phylogenies. Symbols and shading represent contrasts within or between lineages, as in Fig. 5.

Life spans were shorter than adults especially in species with greater leaf longevity (Appendix G), an ontogenetic difference that follows theoretical predictions (Kikuzawa and Ackerly 1999).

Principal components analysis of species traits

Eigenvalues for axis 1 and axis 2 of the principal components analysis of traits of mature trees (Fig. 8A) explained 42% and 18%, respectively, of the total variation. For simplicity, only the first two axes are presented. Species clustered well according to their community affiliation (Fig. 8A), although Quercus falcata, a tall tree from the sandhill community, was more closely associated with hammock species than sandhill species in the PCA. Scrub and hammock species were separated by differences in rhizome resprouting potential, asymptotic height, radial growth rate, native embolism (PLC), maximum hydraulic conductance, and $A_{\text{mass}}$.

Table 7. Correlation coefficients (R) for leaf traits in relation to habitat factors, including species soil preferences and northern range limits (N latitude) and other leaf traits.

<table>
<thead>
<tr>
<th>Habitat factors and leaf traits</th>
<th>Leaf life span</th>
<th>Period of canopy foliation</th>
<th>Leaf size</th>
<th>SLA</th>
<th>$A_{\text{max}}$</th>
<th>$A_{\text{mass}}$</th>
<th>Foliar N (%)</th>
<th>Chlorophyll content</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil NO$_3$-N + NH$_4$-N</td>
<td>-0.17</td>
<td>-0.28</td>
<td>0.57</td>
<td>0.39</td>
<td>-0.02</td>
<td>0.45</td>
<td>0.70</td>
<td>-0.05</td>
</tr>
<tr>
<td>Soil pH</td>
<td>-0.19</td>
<td>-0.46</td>
<td>0.57</td>
<td>0.41</td>
<td>0.03</td>
<td>0.54</td>
<td>0.58</td>
<td>-0.34</td>
</tr>
<tr>
<td>Soil calcium</td>
<td>-0.20</td>
<td>-0.32</td>
<td>0.59</td>
<td>0.38</td>
<td>0.05</td>
<td>0.53</td>
<td>0.69</td>
<td>0.00</td>
</tr>
<tr>
<td>Soil P</td>
<td>-0.25</td>
<td>-0.37</td>
<td>0.60</td>
<td>0.06</td>
<td>0.10</td>
<td>0.44</td>
<td>0.20</td>
<td>0.14</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>-0.20</td>
<td>-0.05</td>
<td>0.35</td>
<td>0.27</td>
<td>0.12</td>
<td>0.44</td>
<td>0.35</td>
<td>0.20</td>
</tr>
<tr>
<td>N range limit</td>
<td>-0.563</td>
<td>-0.723</td>
<td>0.706</td>
<td>0.405</td>
<td>0.048</td>
<td>0.568</td>
<td>0.646</td>
<td>-0.159</td>
</tr>
<tr>
<td>Leaf traits</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chlorophyll content</td>
<td>0.168</td>
<td>0.22</td>
<td>1.00</td>
<td>0.1</td>
<td>-0.512</td>
<td>0.596</td>
<td>0.064</td>
<td>0.019</td>
</tr>
<tr>
<td>Foliar N</td>
<td>-0.456</td>
<td>-0.738</td>
<td>0.733</td>
<td>0.549</td>
<td>-0.095</td>
<td>0.441</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>-0.568</td>
<td>-0.475</td>
<td>0.288</td>
<td>0.33</td>
<td>0.495</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{\text{mass}}$</td>
<td>0.073</td>
<td>0.174</td>
<td>0.005</td>
<td>-0.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLA</td>
<td>-0.66</td>
<td>-0.651</td>
<td>0.345</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf size</td>
<td>-0.38</td>
<td>-0.63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Period of canopy foliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.829</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: R values >0.5 or < -0.5 are shown in boldface.
Fig. 8. (A) Principal components analysis of species traits for mature trees measured in the field. The following traits were used: leaf life span, laminar leaf area (leaf size), carbon assimilation rate on a mass basis ($A_{\text{mass}}$), specific leaf area (SLA), maximum hydraulic conductance ($K_{\text{max}}$), Huber value (Hub Val), whole-shoot transpiration divided by sapwood area (WhShTr), native percentage loss of conductivity (PLC), asymptotic tree height (height), rhizome resprouting potential (RhRespr), outer bark thickness of saplings (bark), wood density, radial growth increment, and seed mass. (B) Eigenvectors indicating direction and magnitude of the weighting of individual traits in the PCA are shown for the same axes as in panel (A). (C) Principal components analysis of species traits for seedlings measured in a common garden. *Quercus alba* (AL), a hammock species, was included in the common-garden experiment, although it does not occur in the field study sites. The following seedling traits were used: leaf life span (LL), laminar leaf area (leaf size), carbon assimilation rate on a mass basis ($A_{\text{mass}}$), specific leaf area (SLA), whole-plant transpiration (WhPlTr), seed mass, absolute growth rate (AGR), and relative growth rate (RGR). Eigenvectors of the traits are shown in panel (D). For (A) and (C), community affiliations, phylogenetic lineages, and habitat types are distinguished by the same symbols and shading as in Figs. 1 and 3. Species codes (from Table 1) are shown next to symbols.

(Fig. 8B). Sandhill species were intermediate between hammock and scrub with respect to these traits. Species that group together in the scrub community, including *Q. minima, Q. pamila, Q. myrtifolia,* and *Q. geminata* have higher rhizome resprouting potential, greater wood density, shorter stature, lower SLA, higher Huber values, and thinner bark than species that group together in the sandhill community, including *Q. laevis, Q. margaretta,* and *Q. falcata.*

The PCA for traits measured on seedlings in the common garden experiment also distinguished between the three community types (Fig. 8C). Again, *Q. falcata* aligned closely to hammock species as well as sandhill species. Scrub and hammock species differed with respect to absolute growth rates, seed size and whole plant transpiration, with hammock species having higher values for these traits (Fig. 8D). Sandhill and hammock species were separated by differences in $A_{\text{mass}}$ and relative growth rates, with sandhill species having lower values for these traits than hammock species. Scrub species had longer leaf life spans, lower SLA, smaller seeds, and smaller leaves than sandhill species (Fig. 8D).

Taking into consideration both the mature tree and seedling analyses, hammock species are characterized by their tall stature, fast growth rates, high hydraulic conductance, high $A_{\text{mass}},$ thin bark, and low rhizome resprouting potential. Scrub species are characterized by high rhizome resprouting potential, low growth rates, short stature, relatively long periods of canopy foliation (although not necessarily long leaf longevities), and thin bark. Finally, sandhill species have thick
bark, short leaf life spans, and are intermediate in many of the traits that distinguish hammock and scrub species.

Analysis of variance for correspondence of traits to community or lineage affiliations

A number of whole plant traits were significantly different among the three communities (Table 8), corroborating the clusters shown by the principal components analyses. According to Scheffe’s post hoc tests, sandhill species had significantly thicker outer bark and greater asymptotic height than scrub species, while scrub species had greater rhizome resprouting potential than the other two groups, and hammock species had greater radial growth rates than the other two groups. Despite low statistical power, two measures of growth rates of seedlings grown under standardized conditions showed differences among species in the different communities (highest for hammock species) when examined using MANOVA ($F_{4,12} = 2.87, P = 0.07$), but there were no differences among phylogenetic lineages ($F_{4,12} = 1.99, P = 1.6$). Variation in leaf-level traits was explained somewhat better by lineage than by community affiliation, with the exception of $A_{\text{max}}$ (Table 8). Significant or marginally significant differences among lineages were found for $A_{\text{max}} (P = 0.006)$, period of canopy foliation ($P = 0.002$), foliar N concentration ($P = 0.004$), SLA ($P = 0.003$), leaf life span ($P = 0.055$), and chlorophyll content ($P = 0.088$). Differences for period of canopy foliation and leaf N were also found among communities, but were less significant. $A_{\text{max}}$ showed significant differences only among communities. For mature trees, $A_{\text{max}}$ was significantly lower for scrub species than hammock species, while period of canopy foliation was significantly longer among scrub species relative to sandhill species and longer in live oaks than in white oaks. In general, traits that were similar within communities were not similar within lineages, and vice versa, with the exception of foliar nitrogen concentration, which was different among communities and among lineages (white oaks had higher leaf N than live oaks) and period of canopy foliation (longer for live oaks than white oaks). Vessel diameters, Huber value (ratio of sapwood area to supported leaf area), and wood density differed among lineages, showing significant evolutionary conservatism, but not among communities (Table 8).

Species diversity in relation to soil resources

The number of woody species per plot increased with soil fertility initially (from less than six to more than ten) and then remained constant with subsequent increases in soil fertility. In contrast, the average number of oak species per plot remained constant (between 3 and 4) across all soil fertility levels, even at very low fertility sites.

**DISCUSSION**

Our results show that oak species are not randomly distributed across the Florida landscape but show clear patterns of ecological sorting and specialization along the major environmental gradients in this region, including soil moisture, soil fertility, and fire regime. Oak species in different habitats possess functional traits that are known a priori to provide advantages for survival in those habitats, and there appear to be fundamental trade-offs in life history and physiological traits that prevent species from performing well across all

Table 8. Univariate ANOVAs for leaf and whole-plant traits with community (three levels) or clade (three levels) treated as the main fixed effects (df = 2, 14).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Community (scrub, sandhill, hammock)</th>
<th>Clade (red, white, live oak)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MS</td>
<td>$F$</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>4.560</td>
<td>0.240</td>
</tr>
<tr>
<td>Chlorophyll content</td>
<td>396.0</td>
<td>0.781</td>
</tr>
<tr>
<td>Vessel diameters</td>
<td>17.49</td>
<td>0.971</td>
</tr>
<tr>
<td>$K_{\text{max}}$</td>
<td>1.326</td>
<td>1.248</td>
</tr>
<tr>
<td>Huber value</td>
<td>1.309</td>
<td>1.383</td>
</tr>
<tr>
<td>SLA</td>
<td>286.9</td>
<td>1.526</td>
</tr>
<tr>
<td>Whole-shoot transpiration</td>
<td>1.673</td>
<td>1.740</td>
</tr>
<tr>
<td>Leaf life span</td>
<td>6825</td>
<td>2.663</td>
</tr>
<tr>
<td>Leaf size</td>
<td>1291</td>
<td>2.761</td>
</tr>
<tr>
<td>Wood density</td>
<td>0.021</td>
<td>3.189</td>
</tr>
<tr>
<td>PLC†</td>
<td>0.058</td>
<td>3.268</td>
</tr>
<tr>
<td>Seed mass</td>
<td>1.297</td>
<td>3.410</td>
</tr>
<tr>
<td>Period of canopy foliation</td>
<td>5762</td>
<td>3.940</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>0.003</td>
<td>5.276</td>
</tr>
<tr>
<td>N (%)</td>
<td>0.412</td>
<td>6.357</td>
</tr>
<tr>
<td>Bark thickness</td>
<td>0.042</td>
<td>14.73</td>
</tr>
<tr>
<td>Asymptotic height</td>
<td>504.5</td>
<td>15.74</td>
</tr>
<tr>
<td>Rhizome resprouting</td>
<td>10.06</td>
<td>35.21</td>
</tr>
<tr>
<td>Radial growth</td>
<td>9.360</td>
<td>17.59</td>
</tr>
</tbody>
</table>

† PLC is percentage loss of conductivity.
environments. Thus, at the landscape scale, i.e., the scale at which major shifts in soil moisture, fertility and fire regime occur (1–100 ha), maintenance of high oak diversity can be explained by niche partitioning of the important environmental gradients. At smaller spatial scales, however, other mechanisms of species coexistence must be invoked (Cavender-Bares et al. 2004).

Species distributions, community structure, and niche partitioning

Soil moisture, soil fertility, and fire regime play an important role in explaining the distributions of oak species in north-central Florida. All soil moisture and soil fertility factors, with the exception of pH, were negatively correlated with the first axis of ordination in the detrended correspondence analyses (Table 2) indicating that species are differentially distributed along a gradient of soil moisture and availability of various nutrients, which covaried to a large extent (Table 3). These results corroborate previous studies in the region indicating that soil resource availability, driven by differences in soil hydrology, is important in the structuring of forest communities (Monk 1965, 1968, Hook 1984, Hodges 1995). Studies of oak species in other regions have also shown that they are distributed differentially across gradients of soil moisture or rainfall (Monk et al. 1989, Knops and Koenig 1994, Villar-Salvador et al. 1997).

Species cluster spatially within three major community types (hammock, scrub, and sandhill) that differ in fire regime (Fig. 2A and B). Fire plays a major role in maintaining oak diversity because both sandhill and scrub communities, which collectively contain eight oak species, are fire dependent. Differences in the severity and frequency of fire maintain these two very distinct fire-dependent communities. In contrast, most hammock species are not fire tolerant and they occur largely where fire is excluded for long periods of time. The strong correlation of the first axis of ordination (Fig. 2A) with fire frequency index indicates that the soil resource gradient and fire frequency covary as a function of soil moisture regimes. Fire frequency and water availability are generally inversely correlated, such that fire frequency increases as water availability or flooding period diminishes (Bonnicksen and Christensen 1981, Swetnam and Betancourt 1990). It is likely that fire patterns reinforce distributions of vegetation corresponding to water availability. However, because the fire frequency index does not include scrub species, the first axis of ordination (Fig. 2A) should be interpreted only as an approximation of fire frequency, with hammock species (low axis scores) having very low frequency fires (on the order of every 100 yr) and scrub and sandhill species (high axis scores) having higher frequency fires (every ~50 yr for scrub; every 1–15 yr for sandhill).

The second axis may be interpreted in terms of fire severity, with scrub species (high axis scores) having high severity canopy fires and sandhill species (low axis scores) having more frequent, low severity ground fires. While soil moisture is weakly correlated with the second axis, soil fertility is not correlated as there are no detectable differences in soil fertility between scrub and sandhill communities. In a series of studies comparing successional patterns after a range of fire exclusion intervals, Myers (1985, 1990) concluded that scrub and sandhill communities are separated by their fire regime, facilitated by the vegetation itself. This interpretation is supported in the present study by the actual fire histories in these communities, to the extent that they are known, and by current fire management practices. Oak species in these two communities differ in various functional traits that are best interpreted to reflect adaptation to contrasting fire regimes as discussed in the section of functional traits below. Hammock species (intermediate axis scores) incur unpredictable fire severity, depending on topography and fluctuations in drought and temperature (Ewel 1990). In the absence of fire, low-fertility sites can become hammock communities that support several of the opportunistic hammock oak species that do not survive fire, including Q. hemispherica and Q. nigra. In addition, oak species that may be fire tolerant in terms of bark thickness but are also competitive in hammock communities (due to tall stature and relatively high growth and photosynthetic rates), including Q. falcata and Q. stellata (intermediate first-axis scores, Fig. 2A), may also be found in low-fertility hammock communities where fire has been excluded. In contrast, some hammock oak species appear to be found only in nutrient/cation rich hammocks (Q. michauxii, Q. shumardii, Q. austrina) or hydric hammocks (e.g., Q. laurifolia). These species tend to be large seeded, to have high hydraulic conductance and gas exchange rates and to be poor resprouters.

Partitioning the abiotic environments

Our results show strong evidence for niche partitioning across major soil resource gradients. Average overlap of species within plots, calculated according to Pianka’s niche overlap (Pianka 1973), was significantly less than expected by chance across all soil factors (Table 4). The lowest overlap values, considering all species pairs, were along soil moisture and pH gradients. In the north-central Florida landscape, niche differentiation among the soil moisture gradient corresponds to the differentiation among fire regimes, as these variables are coupled. Within hammock communities, however, differentiation across the soil moisture gradient is less pronounced than it is for the entire landscape (Fig. 3, Table 4). Hammock species are still significantly differentiated across the pH gradient but also appear to be differentiated with respect to soil calcium (Table 4). The partitioning of the pH and cal-
calcium gradients among hammock species corresponds
to the separation among hammock species on the sec-
tion of the third DCA ordination (Fig. 2B), showing that 
_Quercus shumardii_ and _Q. michauxii_, in particular,
prefer higher pH sites and sites with higher cation avail-
ability than other species.

**Specialization for specific habitats**

Partitioning of the abiotic environment is consistent
with the hypothesis that species have suites of func-
tional traits that allow them to specialize for particular
ranges along resource gradients where they can be most
competitive. A high degree of variation in the abiotic
environment can thus maintain high numbers of spe-
cialists for these environments. Here we discuss evi-
dence for the correspondence of critical functional
traits of species to their habitat preferences for traits
known a priori to be adaptive to particular environ-
ments based on theoretical understanding of their func-
tion and on previous empirical evidence.

**Traits related to fire tolerance.**—Traits related to fire
tolerance and post-fire recovery, such as bark thickness,
rhizome resprouting potential and asymptotic height
are well distinguished among species of the three com-

**Leaf-level traits**

Contrary to expectation and to previously docu-
mented relationships in other systems (e.g., Karlsson
1992, Reich et al. 1992, Wright et al. 2001), leaf-level traits, including leaf life span, period of canopy foliation, specific leaf area, and \( A_{\max} \), were not correlated with any of the soil factors measured, including soil nitrate and ammonium or soil moisture (Table 7), although \( A_{\max} \) was correlated with species habitat preferences for soil pH and soil calcium. The lack of correlation results from the phenomenon that species with contrasting leaf phenologies often occur together, particularly in hammock communities, but also to some extent in scrub communities. In a separate study, leaf life spans of oaks co-occurring within 0.10-ha plots were found to be more contrasting than expected by chance (Cavender-Bares et al. 2004).

Given that the ranges of leaf life spans and other leaf traits are relatively narrow relative to other studies linking leaf traits to nutrient availability (Schlesinger and Chabot 1977, Chabot and Hicks 1982, Reich et al. 1992, 1997, Karlsson 1994, Eckstein et al. 1999, Wright et al. 2001), their lack of correlation with soil fertility is not necessarily surprising. However, leaf-level traits do show correlations with leaf N concentration at the level of individual leaves (Appendix F) and/or at the species level (Table 7). While leaf N cannot be considered a measure of soil fertility, given complexities of interactions between soil moisture and nutrient supply (Wright et al. 2001) and the conservative nature of leaf N within species and within lineages (Table 8), these results leave open the possibility that at small spatial scales (tens of meters) species may be partitioning microenvironments by foraging at different depths. No differences in predawn water potential have been found among species occurring together in this system (Cavender-Bares and Holbrook 2001), although fine root placement could nevertheless be occurring at different depths leading to differential access to nutrient supplies (Goulden 1996, Hooper and Vitousek 1997). Such a mechanism is testable and could contribute to species coexistence at small spatial scales.

Leaf longevity may also be linked to successional status of the species within a given community (Mulkey and Kitajima 1995), as well as to fire regime. Interestingly, the lack of correlation between leaf traits and soil nutrients results partially from the short leaf longevities and deciduous leaf habits of the sandhill species that grow in habitats with low soil resource availability, but with relatively high light availability. This gives rise to significant or marginally significant difference among community types with respect to several leaf traits, including period of canopy foliation (Table 8). Cost–benefit theory of leaf longevity at the leaf and whole-plant level (Kikuzawa and Ackerly 1999, Givnish 2002) suggests that leaf-longevity is a function of time to recover initial investment, which should be shorter under high light and nutrient availability. Frequent fires in sandhill communities maintain relatively open canopies and provide frequent pulses of nutrients (although post-fire nutrient pulses may be rather small; Webber 1935, Abrahamson 1984, Myers 1985). High litter accumulation during the period of deciduousness may encourage fire when the trees are dormant and more tolerant of fire (Glitzenstein et al. 1995), leading to a positive feedback between short leaf longevity and fire frequency. In contrast to sandhill oaks, scrub oaks have more densely arranged foliage, apparently a greater degree of self-shading, and lower daily photosynthetic income per unit leaf mass (J. Cavender-Bares, unpublished data). These traits are apparently coupled with greater leaf longevity and evergreen habit as predicted by cost. Evergreen habits of many scrub and some hammock oaks would be disadvantageous where fire occurs very frequently as in sandhill communities.

In contrast to soil fertility, the northern range limits of species were significantly correlated with leaf longevity, period of canopy foliation, and \( A_{\max} \) (Table 7). Hence, leaf longevities may be more adapted to broader climatic factors, such as the length of the growing season, than to local edaphic factors. As a result, oak species may not be optimally distributed across local soil fertility gradients with respect to nutrient use efficiency. Rather, in the assembly of the current communities, species may have preferentially tracked environmental factors for which they had narrower tolerances (Ackerly 2003), such as fire regime and soil moisture. This hypothesis is supported by the fact that species showed narrower niche distributions across the soil moisture gradient than expected, but not across the nitrate and ammonium or phosphorus gradient (Table 4). Leaf-level traits also tend to be conserved within the major lineages (Table 8), and may not be as evolutionarily labile as other traits, limiting the extent to which leaf traits could have adapted through natural selection to local soil fertility gradients.

**Association of multiple traits in relation to habitat preference**

The DCA ordinations show good correspondence with the grouping of oak species into three main communities—hammock, sandhill, and scrub—distinguished on the first axis by fire frequency and resource availability, and on the second axis by fire intensity. When the first and second axis scores of the species are analyzed as the dependent variables in MANOVA, the distinctiveness of the three communities is significant (Table 5). The community affiliations are also significantly distinguished in terms of species preference for edaphic properties, including soil moisture and nutrient availability (Table 5). Scheffe’s post hoc analyses reveal that these distinctions arise from differences between hammock and scrub species, as well as between hammock and sandhill species, rather than from differences in soil preferences between scrub and sandhill species. This is consistent with other studies that have failed to find consistent chemical differences in soils between the two communities, making fire regime the distinguishing abiotic factor (Myers 1985).
ANOVARs of individual traits show clear differences in species from different communities for a number of traits, particularly life history traits related to fire tolerance and growth (Table 8, Fig. 4). In terms of adult traits measured in situ, scrub and hammock oaks were separated by differences in rhizome resprouting potential, height, radial growth rate, native embolism (PLC), maximum hydraulic conductance, and $A_{\text{max}}$. Sandhill species were intermediate between hammock and scrub species with respect to these traits. Rhizome resprouting and clonal spreading are a defining characteristic of the scrub oaks, in addition to short stature, slow growth, low hydraulic conductance, low rates of gas exchange, and low native embolism. In contrast, the hammock oaks are characterized by tall stature, fast growth, high gas exchange rates, high native embolism, and high hydraulic conductance. Sandhill species tend to have relatively tall stature, and intermediate growth and gas exchange rates. Thick bark is a critical functional trait that distinguishes sandhill species from scrub and hammock species (Fig. 4).

The PCA for traits measured on seedlings in the common garden experiment also distinguished between the three types of community affiliations. Q. falcata aligned closely to hammock species as in DCA analysis. Scrub and hammock species differed with respect to absolute growth rates, and whole plant transpiration, with hammock species having higher values for these traits. Sandhill and hammock species were separated by differences in $A_{\text{max}}$ and relative growth rates, with sandhill species having lower values for these traits than hammock species. Although this analysis includes a smaller number of species, it corresponds well to PCA for traits of mature trees and indicates that the three types of community affiliations are differentiated by growth-related traits.

Interpreting trait–environment correlations

One difficulty in interpreting trait–environment correlations in field studies is that the differences in traits between species may be the result of both genetic differences and plasticity if species are measured in different environments. Common garden experiments can help determine the extent to which trait differences observed among species in the field are genetic vs. environmentally induced (Givnish et al. 2004). Practically, however, it is very difficult to adequately reproduce all of the representative field conditions in a common garden. Moreover, many traits cannot be measured on seedlings, making the study of long-lived species particularly challenging. In our study, the high degree of correlation between traits measured in the field and in the common garden indicates that trait differences among species measured on mature trees in the field have a strong genetic component and are not merely the result of plasticity in traits of species that have contrasting distributions. There were important differences in magnitude between seedlings and adults for some of the traits, but the relative ranking of the species was similar (Appendix G). This result is important given that ontogenetic shifts in traits can be significant in oaks (Cavender-Bares and Bazzaz 2000), and it gives us confidence in the interpretation of niche differentiation as an explanation for co-occurrence because trait differences among species appear to have a genetic basis.

The relative importance of maternal effects in the common garden experiment is unknown. However, the intraspecific variation in seed size, which is one measure of maternal effects (Sultan 1996), was small relative to the variation across species (Fig. 5). Given that seeds were collected from a range of sites and that mean seed sizes compare well with previously published ranges, it is likely that seed size, itself, reflects an intrinsic property of the species. Nevertheless, the role of maternal effects in influencing species distributions is an important issue warranting further study.

Explaining oak diversity at smaller spatial scales

At large spatial scales (1–100 ha), environmental heterogeneity supports a high number of oak species specialized for different habitats. At smaller spatial scales, where soil moisture, fertility and fire regime are not changing significantly (i.e., within 0.1-ha plots), other mechanisms must be invoked to explain the co-occurrence of multiple oak species. In many systems, increasing soil fertility permits increasing biological diversity until a saturation point is reached (e.g., Huston 1994, Cornwell and Grubb 2003). In this system, it also appears that increasing nutrient supply permits increases in diversity of woody plants, particularly at the low end of the soil fertility gradient (Fig. 9). However, the same pattern is not shared by the oaks, which maintain a constant number of oak species per 0.1-ha plot across the entire soil fertility gradient (Fig. 9) as well as across communities (not shown). This suggests that there is a limit to the maximum diversity of oak species at small spatial scales that cannot be explained by resource availability, other abiotic factors, or community composition.

We suggest that within the oak genus, phylogenetic diversity may control the maximum number of oaks that can occur together at small spatial scales. In a related study, Cavender-Bares et al. (2004) provide strong evidence that these communities show a distinct pattern of phylogenetic overdispersion, whereby oak species from different lineages (more distantly related) are more likely to occur together than species from the same lineage (more closely related). This can be viewed to some extent in Fig. 2A and B, which shows that in all communities, species from different phylogenetic lineages are represented. Among the regional species pool of oaks, it appears that there is sufficient phylogenetic diversity to allow the co-presence of three or four oak species per plot, regardless of the abiotic environment or local species composition. Within plots,
Conclusions

This study provides strong evidence that at the landscape scale niche partitioning and habitat specialization contribute to the coexistence and maintenance of high diversity within the oak genus in north-central Florida. We have shown that species exhibit less overlap in their distributions across environmental gradients than expected and that species show significant differentiation in functional traits that allow them to specialize for contrasting physical environments, particularly with respect to fire frequency and severity, soil moisture, and soil fertility. Three previously described community types—hammock, sandhill, and scrub—are clearly distinguished by species composition, the abiotic environment, and the functional traits of the oak species in them. Species within the three major phylogenetic lineages of oaks represented in Florida are distributed across these communities and environmental gradients, exhibiting evolutionary convergence in habitat preferences. This pattern of phylogenetic overdispersion and evolutionary convergence is explored in detail in a related study (Cavender-Bares et al. 2004) and may explain coexistence of multiple oak species at small spatial scales. While the results presented here do not preclude other mechanisms of coexistence, they provide a strong case for habitat differentiation at the landscape level (1–100-ha scale) and an explanation for both species diversity and functional diversity.

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APPENDIX A
A list of non-oak woody species used in the gradient analyses is available in ESA’s Electronic Data Archive: Ecological Archives M074-014-A1.

APPENDIX B
A table showing leaf-level traits for 17 oak species is available in ESA’s Electronic Data Archive: Ecological Archives M074-014-A2.

APPENDIX C
A table showing whole-plant traits for 17 oak species is available in ESA’s Electronic Data Archive: Ecological Archives M074-014-A3.

APPENDIX D
A table of seedling biomass equations as a function of other measured variables for calculation of relative growth rate (RGR) is available in ESA’s Electronic Data Archive: Ecological Archives M074-014-A4.

APPENDIX E
Species pairwise niche overlap values across a soil moisture gradient are presented in ESA’s Electronic Data Archive: Ecological Archives M074-014-A5.
APPENDIX F

Graphs showing leaf trait relationships for individual leaves for $A_{\text{max}}$, SLA, and %N are presented in ESA’s Electronic Data Archive: *Ecological Archives* M074-014-A6.

APPENDIX G

Graphs showing the relationship between traits measured on seedlings grown in a common garden and traits measured on mature trees measured in the field are presented in ESA’s Electronic Data Archive: *Ecological Archives* M074-014-A7.