PHYLOGENETIC STRUCTURE OF FLORIDIAN PLANT COMMUNITIES DEPENDS ON TAXONOMIC AND SPATIAL SCALE

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Abstract. Consideration of the scale at which communities are defined both taxonomically and spatially can reconcile apparently contradictory results on the extent to which plants show phylogenetic niche conservatism. In plant communities in north central Florida, we collected species abundances in 55 0.1-ha plots in several state parks. When communities were defined narrowly to include a single phylogenetic lineage, such as *Quercus*, *Pinus*, or *Ilex*, neighbors tended to be less related than expected (phylogenetic overdispersion) or there was no pattern. If the same communities were defined more broadly, such as when all seed plants were included, neighbors tended to be more related than expected (phylogenetic clustering). These results provide evidence that species interactions among close relatives influence community structure, but they also show that niche conservatism is increasingly evident as communities are defined to include greater phylogenetic diversity. We also found that, as the spatial scale is increased to encompass greater environmental heterogeneity, niche conservatism emerges as the dominant pattern. We then examined patterns of trait evolution in relation to trait similarity within communities for 11 functional traits for a single phylogenetic lineage (*Quercus*) and for all woody plants. Among the oaks, convergent evolution of traits important for environmental filtering contributes to the observed pattern of phylogenetic overdispersion. At the broader taxonomic scale, traits tend to be conserved, giving rise to phylogenetic clustering. The shift from overdispersion to clustering can be explained by the increasing conservatism of traits at broader phylogenetic scales.

Key words: environmental heterogeneity; Florida; Ilex; niche conservatism; overdispersion; phylogenetic structure of communities; Pinus; Quercus; taxonomic scale; trait convergence.

Introduction

There is growing recognition that species evolve within communities and that community interactions influence the evolutionary process (Antonovics 1992, Neuhauser et al. 2003, Whitham et al. 2003). At the same time, we are becoming increasingly aware that evolutionary processes, particularly the way that traits evolve within lineages, influence species distributions and assembly in communities (McPeek 1996, Webb et al. 2002, Ackerly 2003, Chazdon et al. 2003, Cavender-Bares et al. 2004*a*). This study seeks to understand the role that trait evolution plays in determining the phylogenetic structure of communities and the extent to which phylogenetic structure depends on how communities are defined.

Two processes are often considered as central to the assembly of communities: (1) filtering of species that can persist within a community on the basis of their tolerance of the abiotic environment (e.g., Weiher and Keddy 1995), and (2) competitive interactions among species that limit their long-term coexistence (Elton

1946, MacArthur and Levins 1967, Chesson 1991, Leibold 1998). The two processes lead to opposite predictions about the phenotypic similarity and phylogenetic relatedness of co-occurring species (Tofts and Silvertown 2000, Webb et al. 2002). If closely related species share similar physiological limitations and exhibit evolutionary niche conservatism, environmental filtering will tend to cause closely related species to co-occur (phylogenetic clustering). In contrast, competitive exclusion should limit the coexistence of closely related species if species compete for the same limiting resources, leading to the opposite pattern of phylogenetic overdispersion. Both processes can operate simultaneously in real communities, but have greater influence at different scales. Keddy and Weiher (1999) hypothesized that limiting similarity should have greater importance at smaller spatial scales, whereas environmental filtering should predominate at larger spatial scales. Evidence supporting this view has been found in meadow communities in Great Britain (Silvertown et al. 2005).

At the same time, the ecological process that appears to predominate might also depend on how broadly or narrowly communities are defined. For example, phylogenetic clustering was found among tree species in rainforest communities in Borneo (Webb 2000), as well as in herbaceous communities in Great Britain (Tofts

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A) Phylogenetic structure of communities

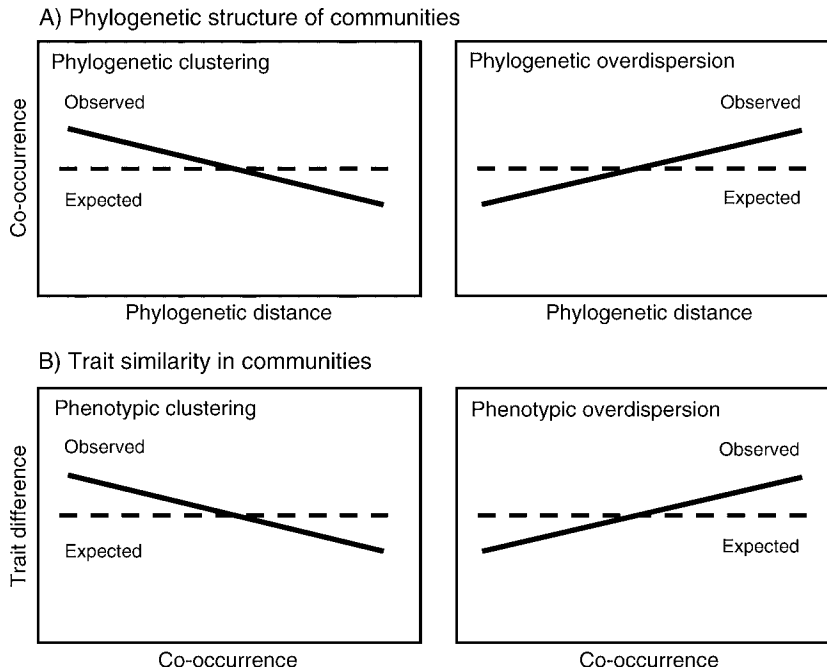B) Trait similarity in communities

FIG. 1. (A) Phylogenetic structure of communities. An observed correlation (solid line) that is more negative than expected (dashed line) indicates phylogenetic clustering (left panel), because closely related species occur together more often than expected by chance; an observed correlation that is more positive than expected indicates phylogenetic overdispersion (right panel), because closely related species do not occur together. (B) Trait similarity in communities. An observed correlation that is more negative than expected indicates that co-occurring species show similar trait values (phenotypic clustering, left panel); an observed correlation that is more positive than expected indicates that trait values can be highly variable within communities (phenotypic overdispersion, right panel).

and Silvertown 2000). Both studies considered a large number of angiosperm lineages, providing support for the generalization that evolutionary stasis, or phylogenetic niche conservatism, is widespread among plant communities around the globe (Harvey and Pagel 1991, Eldridge 1995, Wen 1999, Webb et al. 2002, Ackerly 2003, Qian and Ricklefs 2004). In contrast, phylogenetic overdispersion has been found in narrowly defined communities that include a single phylogenetic lineage, including within Caribbean lizard communities (Losos et al. 2003) and among co-occurring oaks in north central Florida (Cavender-Bares et al. 2004a). In the latter study, evidence of convergence, rather than conservatism, in the evolution of species niches highlighted the prevalence of species interactions over niche conservatism in community assembly. These studies suggest that patterns of phylogenetic dispersion might vary systematically with taxonomic scale. The present study seeks to evaluate this possibility by examining the vegetation of Florida at various taxonomic and spatial scales. In addition, the study addresses the role that trait evolution plays in the phylogenetic structure of communities. Specifically, we make the following predictions:

1) The pattern of phylogenetic structure among communities depends on how a community is defined in terms of the taxa included. The more broadly a community is defined, the more likely it will be to show phylogenetic clustering as a result of trait conservatism

and environmental filtering. Narrowly defined communities, in contrast, are more likely to show phylogenetic overdispersion, either as a result of trait convergence, trait overdispersion, or both.

2) The phylogenetic structure of communities depends on the spatial scale of the analysis. As the spatial scale is increased to encompass greater environmental heterogeneity, species interactions should become less important, and phylogenetic clustering should emerge as the dominant pattern.

3) The relationship between trait evolution (conservative vs. convergent) and trait similarity within communities (clustered vs. overdispersed) should predict the phylogenetic structure of communities at different scales of analysis.

MATERIALS AND METHODS

Tests of phylogenetic structure of communities

We examined the phylogenetic structure of communities by comparing the degree of co-occurrence of species pairs in relation to the phylogenetic distance between them (Fig. 1A). Due to nonindependence and non-normality of the data points, these correlations were compared to null models. Tests for phylogenetic clustering and overdispersion were conducted for a suite of different data sets in north central Florida and in the entire state of Florida that vary in spatial extent and

resolution of data. We compared the correlation coefficient of the relationship between co-occurrence and phylogenetic distance of species pairs to a null model in which either species distributions were permuted or phylogenetic relationships among species were randomized (Fig. 1A; Cavender-Bares and Wilczek 2003). The pairwise values of co-occurrence (C) were calculated based on proportional similarity (Schoener 1970) as follows: $C_{ih} = 1 - 0.5 \Sigma |p_{ij} - p_{hj}|$, where C_{ih} is the co-occurrence of species i and h, and p_{ij} is the proportion of total basal area or the proportion of occurrences of the ith species in the jth plot. We calculated phylogenetic distances from the estimated intervening branch length distances (measured in millions of years) between species pairs based on community phylogenies created for each test (see *Phylogenetic analyses*).

Three null models were used. The first two generated a null distribution of expected species occurrence patterns against which to compare the observed data. These allow us to ask the following question: Given the evolutionary history of the taxa in the regional species pool, does phylogenetic relatedness influence the way that species have assembled in communities? In null model 1, basal area of species within plots was randomized by reshuffling raw data values 999 times across plots, but constraining the total basal area per species. Null model 2 used presence/absence data, instead of basal area, and constrained both total occurrences per species and total number of species per plot, using the sequential swap algorithm (Gotelli and Entsminger 2001b). The null model for the presence/absence data may be the most biologically realistic, because it constrains both species abundances and plot diversity levels (Gotelli and Graves 1996). However, presence/absence data provide a lower degree of resolution for the distributions of species than basal area, because differences in relative abundance within plots are not considered. A null model that constrains total basal area per species and plot would probably be impossible to construct and was not attempted. Randomizations were carried out using Ecosim (Gotelli and Entsminger 2001a), and the co-occurrence vs. phylogenetic distance correlations were carried out in a self-written Visual Basic program, modified to accommodate large data sets from Cavender-Bares et al. (2004a).

A third null model kept constant the distribution of species within communities, but randomized the phylogenetic tree topology. Null model 3 allows us to ask, given the distribution of species in communities, does the phylogenetic relatedness of species within those communities differ from random expectation? To randomize, we used the "random branch moves" algorithm in Mesquite (Maddison and Maddison 2000) and assigned the number of branch moves to equal the number of taxa in the tree. The total branch length distance from the basal node to the tips was kept constant. A distance matrix was then automatically computed from each of the 999 randomized trees, as well as from the original phylogeny, using a program in Visual Basic (J. Cavender-Bares, *unpublished software*). We used the result of this computation to calculate a null distribution of correlation coefficients between pairwise species co-occurrence and phylogenetic distance. In all analyses, a P value was calculated based on a two-tailed test. Since the null models use 999 randomizations plus the observed value, the minimum P value is 0.002 (Manly 1991).

Trait similarity within communities

We used a similar test to examine trait similarity within communities (Fig. 1B) by comparing the absolute value of pairwise differences in trait values to the degree of co-occurrence between species pairs. The observed correlation coefficients were tested against null model 2, in which the presence/absence of species within plots was randomized keeping row and column totals constant. The ranking of the observed correlation coefficient relative to that of the null model provides a way to order the measured traits in terms of their similarity within communities. The term "phenotypic clustering" refers to high trait similarity within communities, while the term "phenotypic overdispersion" refers to low trait similarity within communities (Fig. 1B)

The spatial extent of communities

In order to test the importance of (1) the spatial resolution of data, and (2) how communities are defined, we analyzed a series of community data sets that differ in the resolution of species abundances and in the community definition. First, we examined the influence of using basal area or presence/absence to evaluate species abundance in random 0.1-ha plots of north central Florida. Second, we examined the influence of the way community boundaries are defined by using these random 0.1-ha plots, where community boundaries are fixed by a standard area (hereafter referred to as the plot survey), or by using previously established community classifications and vegetation maps within state parks (hereafter referred to as community classifications). In the latter case, community boundaries in north central Florida were defined by environmental variation and the vegetation itself according to the Florida Natural Areas Inventory and the Florida Department of Natural Resources (FNAI and FDNR 1990). Previously determined community classifications for the entire state of Florida were also used, so that environmental variation among communities encompasses topographic and edaphic variation, as well as climatic variation.

To examine the influence of the inclusion or exclusion of communities on phylogenetic structure, we performed tests of co-occurrence vs. phylogenetic distance for three individual genera (*Quercus*, *Pinus*, and *Ilex*), using community classification data sets for six state parks in north central Florida relative to two null models (both

corresponding to null model 2). We created the first null model by permuting the presence of species across only those communities that contained a member of the genus (no community had zero as a matrix element). We created the second null model by permuting species' presences across all communities that existed in the six parks examined, regardless of whether any members of the genus were found in them or not (a number of communities were represented by zeros in the matrix). This allowed us to test whether increasing the number of communities (effectively increasing the spatial scale and the degree of environmental heterogeneity) would alter the results.

Inclusiveness of taxa within communities

To examine the influence of phylogenetic scale, or the inclusiveness of taxa, on phylogenetic structure of communities, we carried out the same tests for the plot survey data to examine the phylogenetic structure of plant species within communities for (1) species within a monophyletic lineage (Quercus), (2) all angiosperms in the same guild (tree and shrub strata), (3) all plants in the tree and shrub strata, and (4) all recorded plants in all strata, including trees, shrubs, vines, epiphytes, and herbaceous species. These were tested against null models 1, 2, and 3, and against null models 2 and 3 only in the latter case, as only presence/absence data were available. We ran the same tests for the community classification data. The three most diverse woody plant genera within north central Florida, including the oaks (18 species), the hollies (seven species), and the pines (six species), were included to examine lineage-specific patterns in the context of their biogeographic and evolutionary history.

Trait similarity within communities in relation to trait evolution

For suites of life history and functional traits, we used the relationship between trait conservatism and trait similarity within communities to understand the phylogenetic structures of communities for the oaks only, as well as for all trees and shrubs in the plot survey. Trait similarity within communities was determined from the correlation of trait differences between species pairs and their degree of co-occurrence, relative to null model 1 (Fig. 1B). Trait conservatism (or phylogenetic signal) was calculated using methods developed by Ackerly in the "Analysis of Traits" module in Phylocom (Webb et al. 2004), based on trait differences between nodes, normalized by the standard deviation of the trait within a given lineage relative to a null model in which species are randomized across the phylogeny (Moles et al. 2005). We used the ranking of the observed phylogenetic signal relative to the simulations of the null model to order the traits by their degree of conservatism. We recognize that measures of trait conservatism are influenced by taxon sampling and might be biased in highly pruned phylogenies, such as

those used in the present study (Ackerly 2000). Nevertheless, examination of patterns of trait evolution with increasing taxonomic diversity is useful for understanding how trait conservatism shifts with phylogenetic scale in a single study system.

Trait data collection

We measured a suite of leaf traits on mature trees across the range of their local environmental distributions, collected from five state and city parks in north central Florida, including San Felasco Hammock State Preserve, Ichetucknee Springs State Park, Morning Side Nature Center, Payne's Prairie State Preserve, and O'Leno State Park. For five individuals of each species, three sun and three shade leaves from each individual were measured for leaf area, scanned, and dried for leaf mass. We then used scanned leaf images to calculate perimeter (P), the perimeter-to-area ratio (P/A), which has been shown to be correlated with leaf hydraulic conductance (Sack et al. 2003), and lobedness (PL/A), determined as the perimeter-to-area ratio, scaled by leaf length (L). In addition, we took plant height, seed mass, and cotyledon type (photosynthetic or storage cotyledons), which has been shown to influence growth dynamics (Kitajima and Fenner 2000), from published (Kurz and Godfrey 1962, Mirov 1967, Schopmeyer 1974, Godfrey and Wooten 1981, Wenger 1983, Godfrey 1988) or online sources. We were able to collect leaf trait data for 90 of the 122 species examined in the plot survey; maximum height and leaf habit were obtained for 115 species, seed mass for 63 species, and cotyledon type for 87 species.

It is useful to include as many different kinds of traits as possible that might contribute to ecological filtering and interactions among species. The present study, however, examined a limited number of easily measured traits. A suite of additional traits, including maximum hydraulic conductivity, vessel diameter, wood density, leaf longevity, and others were available from previous studies for the Quercus species (Cavender-Bares and Holbrook 2001, Cavender-Bares et al. 2004b), and these are presented in the oak analysis for comparison.

Community data collection

Plot survey data in north central Florida.—Quantitative vegetation data were collected from randomly located 20 × 50 m (0.1 ha) plots established in a previous study (Cavender-Bares et al. 2004a, b) in several state parks in north central Florida. Seventy four plots were originally established in 1998 for a study on oaks, and 55 of these original plots were resampled to determine the basal area of all woody species as well as the presence/absence of all plant species common enough within a plot to be conspicuous. Insufficient time and inability to relocate some of the plots prevented a complete resampling of all of the original plots. Within each plot, the diameter at breast

height of each tree over 1 m height was measured for calculation of basal area for a total of 122 tree and shrub species (see Appendix A). The presence/absence of all seed plants was also recorded for each of the plots (141 species; see Appendix A). The majority of the plots are located in three state parks, including San Felasco Hammock State Preserve (28 plots), a 2803-ha park in Alachua County; Ichetucknee Spring State Park (13 plots), a 921-ha park bridging Columbia and Suwanee counties and bisected by the Ichetucknee River; and Manatee Springs State Park (12 plots), a 960-ha park abutting the Suwanee River in Levy County. Two more plots were resampled at other sites in the region, including one at Morning Side Nature Center and one at Paynes Prairie Preserve State Park. An effort was made to sample across a range of the major woody plant community types in north central Florida.

Community classification data in north central Florida.—We obtained species lists for each of six state parks in north central Florida and corresponding maps of natural community types from the District 2 Park Service in Gainesville, Florida, USA. Parks included San Felasco Hammock, Ichetucknee Springs, O'Leno State Park, Big Shoals State Park, Stephen Foster State Park, and Goldhead Branch State Park. In Florida, 63 terrestrial natural communities were identified and defined by the Florida Natural Areas Inventory and Florida Department of Natural Resources (FNAI and FDNR 1990), 29 of which occur in terrestrial areas of these state parks in north central Florida. Aquatic communities, which comprised nearly half of the defined communities, were excluded from the analyses because plant species were either poorly represented or poorly documented. A natural community is defined by the FNAI and FDNR (1990) as a "distinct and reoccurring assemblage of populations of plants, animals, fungi, and microbes naturally associated with each other and their physical environment." In each park, we assigned species to designated communities, either by data directly from the Park Service or from a master list from the FNAI and FDNR (1990). If community assignments were not available from these sources, we determined them from two other sources (Kurz and Godfrey 1962, Godfrey 1988). Data were sufficient to include only the tree and shrub species (216 species). There were 29 possible community types, replicated according to whether they occurred in multiple state parks, giving a total of 75 sample communities used for the community classification analysis.

Community classification data for the state of Florida.—A master species list with the community affiliations of these species was developed for the entire state of Florida from the FNAI and FDNR report. We ran two analyses: one for all listed plant species with identified community types (383 species), and a second for plants in the tree and shrub guild only (255 species) (see Appendix A). We included 50 terrestrial commun-

ities in the analyses, including wetlands and coastal communities. Unlike the analyses for the parks in north central Florida, each community was represented only once, regardless of how commonly it occurs.

Phylogenetic analyses

Phylogenetic reconstruction.—Community phylogenies were created for each test using Phylomatic (Webb and Donoghue 2005). Phylomatic is an online application for creating a backbone phylogeny based on family and genera.[2] The maximally resolved seed plant tree used for our trees relies on the online resource continually updated by P. F. Stevens, i.e., Angiosperm Phylogeny.[3] Sources for tree construction down to the family level are extensively documented on this web site, although phylogenies created through the Phylomatic maximally resolved seed plant tree are not entirely resolved to the family level. We used a supertree of the angiosperms (Davies et al. 2004) to manually resolve all trees to the family level. Higher taxa were resolved according to published phylogenies (see Appendix B). If no published information was available to resolve polytomies, they remained unresolved. (See Appendix C for all reconstructed phylogenies.) It is important to recognize that the community phylogenies generated using this approach represent only approximations of true species relationships and should be refined as more data and other methods for constructing supertrees become available. The *Quercus* phylogeny was based on Cavender-Bares et al. (2004a) and was consistent with Manos et al. (1999). The four most parsimonious trees from that analysis were tested, as well as several less resolved phylogenies that collapsed nodes with low bootstrap support. We converted branch lengths to millions of years. A less resolved topology was used in the analyses presented here (see Appendix C), but the results were indistinguishable from those using the more resolved phylogenies (data not shown). We based the *Ilex* phylogeny on Cenoud (2000), and the *Pinus* phylogeny on Millar (1993), Schwilk and Ackerly (2001), Grotkopp et al. (2004), and Gernandt et al. (2005).

Branch length estimation.—Branch lengths were based on minimum ages of nodes determined for genera, families, and higher orders from fossil data, and we extrapolated to higher order branches by spacing undated nodes in the tree evenly between dated nodes. This was done using an averaging algorithm in Phylocom (Webb et al. 2004) called "BLADJ" (Branch Length ADJustment, *available online*).[4] Most of the node ages at the family level were taken from Wikström et al. (2001). At the genus level, we used additional sources, including Daghlian and Crepet (1983) for *Quercus*, based on the first appearance of the genus in

TABLE 1. Tests for patterns of phylogenetic structure for community data sets that vary in how communities are defined. For each data set, the number of taxa, the number of communities, the data type (basal area or presence/absence), and the null model used in the analysis are given.

Data type and taxa included	Communities	No. taxa	No. communities	Data type	Null model	r (observed)
North central Florida						
Plot survey data (three parks, 55 plots)						
Quercus species	all	17	55	basal area	1	0.184
Quercus species	all	17	55	pres/abs	2	0.157
Quercus species	all	17	55	basal area	3	0.184
Quercus species	all	17	55	pres/abs	3	0.157
Angiosperm trees and shrubs	all	113	55	basal area	1	−0.030
Angiosperm trees and shrubs/no oaks	all	96	55	basal area	1	−0.019
All tree and shrub species	all	122	55	basal area	1	−0.036
All tree and shrub secies	all	122	55	pres/abs	2	−0.043
All tree and shrub species	all	122	55	basal area	3	−0.036
All tree and shrub species	all	122	55	pres/abs	3	−0.043
All angiosperms	all	130	55	pres/abs	2	−0.008
All angiosperms/no oaks	all	113	55	pres/abs	2	−0.014
All plant species	all	141	55	pres/abs	2	−0.027
All plant species	all	141	55	pres/abs	3	−0.027
North central Florida						
Community classification data (six parks, 29 terrestrial community types)						
Quercus species	all	18	75	pres/abs	2	0.153
Quercus species	oak only	18	38	pres/abs	2	0.153
Quercus species	all	18	75	pres/abs	3	0.153
Pinus species	all	6	75	pres/abs	2	−0.284
Pinus species	pine only	6	29	pres/abs	2	−0.284
Pinus species	all	6	75	pres/abs	3	−0.284
Ilex species	all	7	75	pres/abs	2	0.243
Ilex species	holly only	7	35	pres/abs	2	0.243
Ilex species	all	7	75	pres/abs	3	0.243
Angiosperm trees and shrubs	all	204	75	pres/abs	2	−0.046
Angiosperm trees and shrubs	all	204	75	pres/abs	3	−0.046
All tree and shrub species	all	216	75	pres/abs	2	−0.015
All tree and shrub species	all	216	75	pres/abs	3	−0.015
State of Florida						
Florida community classifications (50 terrestrial community types)						
All tree and shrub species	all	255	50	pres/abs	2	−0.023
All species	all	383	50	pres/abs	2	−0.057

Notes: Observed and expected correlation coefficients (r) for the relationship between co-occurrence and phylogenetic distance of species pairs are shown. P values (two-tailed test) are determined from a null distribution of 999 randomizations plus the observed value.

the Americas, and Cenoud et al. (2000) for *Ilex*, based on the Eocene radiation of the genus, not the earliest appearance of extinct basal lineages. Higher level branch lengths, if available, were converted to millions of years, based on the fossil age for the deepest node. This method of branch length calculation provides only a first approximation of relative evolutionary distances between species. However, given that molecular data could not be used for branch length estimation, this method is an improvement over using only the tree topology itself.

RESULTS

Plot survey data

Oak species: basal area vs. presence/absence.—*Quercus* species showed significant phylogenetic overdispersion when we compared pairwise co-occurrence values to phylogenetic distances and used null models 1 or 3 with basal area (Table 1, Fig. 2A). We obtained similar results when using presence/absence data, rather than basal area, and applying null models 2 or 3, although the results were somewhat less statistically significant (Table 1). These results are very similar to previous analyses (Cavender-Bares et al. 2004a), despite reduced sampling and a less resolved phylogeny.

Increasing taxonomic inclusiveness.—The effect of increasing the number of species in the community analysis was examined with data sets that included angiosperm trees and shrubs, all trees and shrubs, all recorded angiosperm species, and all recorded plants (Table 1). When angiosperm tree and shrub species were included, we found no pattern to the data. This result did not change significantly if we excluded oaks from the analysis. However, the observed correlation coefficient became more negative than 818 of the simulated r values, up from only 650 (Table 1), indicating a shift toward greater clustering. When examining all tree and shrub species (122 species), again using basal area and

TABLE 1. Extended.

r (expected)	Obs>Sim	P	Phylogenetic pattern
0.014	8	0.016	overdispersion
0.004	31	0.064	weak overdispersion
−0.024	1	0.002	overdispersion
0.019	33	0.066	weak overdispersion
−0.025	650	0.700	no pattern
−0.006	818	0.364	no pattern
−0.009	979	0.042	clustering
−0.010	977	0.046	clustering
0.005	992	0.016	clustering
0.009	997	0.006	clustering
−0.009	578	0.844	no pattern
0.008	990	0.020	clustering
−0.014	999	0.002	clustering
0.005	960	0.080	weak clustering
0.013	45	0.090	weak overdispersion
0.028	1	0.002	overdispersion
−0.014	9	0.018	overdispersion
−0.424	254	0.508	no pattern
−0.135	465	0.930	no pattern
0.005	943	0.114	no pattern
−0.029	109	0.218	no pattern
−0.062	34	0.068	weak overdispersion
0.005	175	0.350	no pattern
0.005	999	0.002	clustering
0.038	999	0.002	clustering
0.005	998	0.004	clustering
0.026	979	0.042	clustering
0.021	999	0.002	clustering
0.005	999	0.002	clustering

either null model 1 or 3, a clear pattern of phylogenetic clustering emerged. A nearly identical result was obtained when presence/absence and null models 2 or 3 were used. When all recorded plant species were examined (141 species), the pattern of phylogenetic clustering became even more significant using null model 1. All recorded angiosperm species (130 species) showed no pattern. However, upon removal of the 17 oak species from the analysis, the angiosperms were also significantly clustered. We obtained very comparable results for the two types of null models (community randomizations vs. phylogeny randomizations) (Table 1), although we did not attempt an exhaustive comparison.

Community classification data

In general, similar results were obtained when community classifications were used, rather than actual plot survey data. Based on the community classification, angiosperm trees and shrubs, as well as all trees and shrubs, showed significant phylogenetic clustering. Oaks still showed a pattern of phylogenetic overdispersion

(Table 1, Fig. 2B). This pattern was marginally significant if all communities were used in the analysis and became highly significant if communities where oaks did not occur were excluded from the analysis. One difference that is apparent between the plot survey and the community classification is that closely related oak species show higher degrees of co-occurrence when the community classification is used (Fig. 2A, B). This is not surprising, given that defined community types necessarily include all species that regularly occur in them, and they do not take into account spatial distances among individuals or smaller scale environmental variation that might occur within community types. Despite this difference, the overall pattern of phylogenetic overdispersion in the oaks was clear in both analyses.

The hollies, although much less diverse, showed a similar but only marginally significant pattern of overdispersion, based on null model 2 only (Fig. 2C), due in large part to the non-co-occurrence of pairs of close relatives, i.e., *Ilex cassine* and *Ilex opaca*, as well as *Ilex ambigua* and *Ilex decidua*. Note, however, that the overdispersion pattern was only apparent if community types that did not include any *Ilex* species were excluded from the analysis. The pattern was not significant using null model 3. The pines, a much older lineage, showed a somewhat different pattern (Fig. 2D). The two closest relatives, *Pinus palustris* and *Pinus taeda* (subsection *Australes*), do not co-occur, similar to the pattern in the other two genera. However, at the other extreme, distantly related pines also do not occur. *Pinus clausa,* which is in a different subsection of the genus (*Contortae*) from all of the other pines in the region (section *Australes*), does not co-occur with any other *Pinus* species.

Extending the analysis to communities for the entire state of Florida, a clear pattern of phylogenetic clustering emerged (Table 1). At this scale, which includes coastal and subtropical communities, there is an increase in the number and variety of community types and the degree of environmental heterogeneity that is encompassed. Correspondingly, the number of taxa also increases. Acknowledging the incompleteness of the species list, the number of plant species for the entire state more than doubles that of the north central Florida communities. The large spatial scale and high environmental heterogeneity, along with the greater inclusiveness of taxa, leads to a highly significant pattern of phylogenetic clustering.

Trait evolution and trait similarity within communities

Analysis of trait evolution for the leaf data and life history attributes for the 120-species data set from the plot survey showed that all traits examined were significantly conserved (Fig. 3A). A subset of these traits also showed high similarity within communities (clustering), including specific leaf area for both sun and shade leaves, leaf habit, maximum height, leaf perimeter-to-area ratio, and cotyledon type.
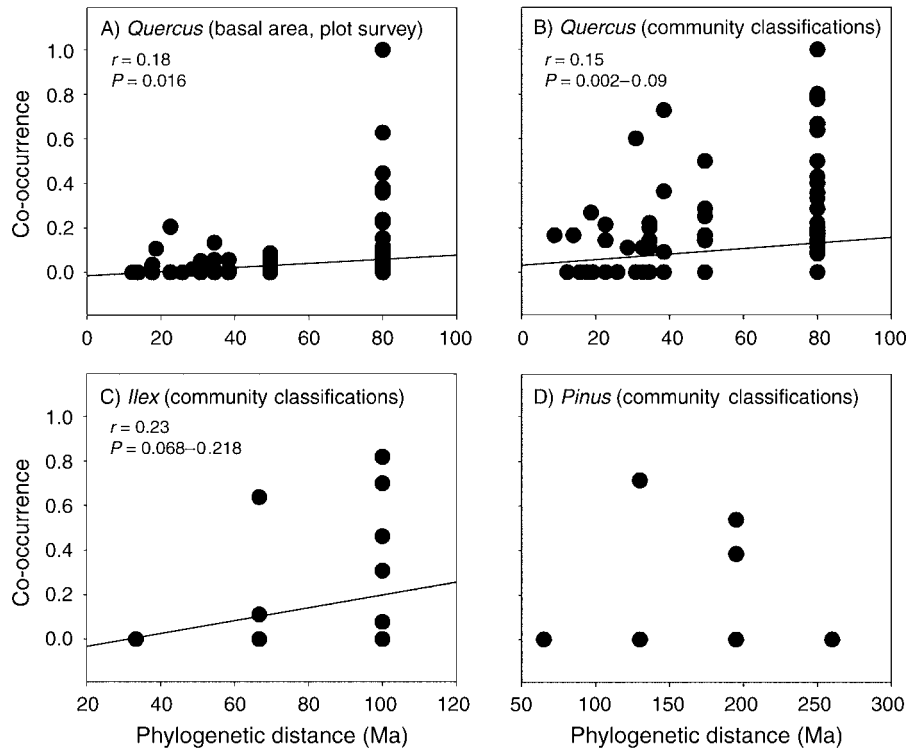
FIG. 2. Results of tests for phylogenetic overdispersion or clustering within three lineages in north central Florida. (A) There is a higher than expected correlation between pairwise co-occurrence (based on measurements of basal area of species within 55 0.10-ha plots) and phylogenetic distance (measured in millions of years [Ma], based on fossil records) for oak species. Closely related species tend not to co-occur, whereas species from different lineages do tend to co-occur. (B) A similar pattern emerges when the analysis is based on presence/absence of oaks in defined community types (based on community classification data) within six state parks in the same region. The significance of the depicted relationship is dependent on whether the null model only includes communities in which oaks occur, or whether all defined terrestrial communities found in the parks are included. (C) A similar, but less significant pattern is found for the less speciose *Ilex* genus. (D) The *Pinus* genus shows a different pattern. Note that in all graphs multiple data points may be superimposed.

In contrast, when the same traits were examined only for the oaks, many fewer traits showed conservatism (Fig. 3B). Conserved traits included leaf mass, leaf area, leaf habit, seed mass, and cotyledon type. None of these traits showed high similarity within communities. Other traits showed a lack of conservatism, which can also be interpreted as various degrees of convergence. Maximum height was the most convergent of the traits examined in this study. The high convergence results from the fact that in each of the major oak lineages, including the red oaks, the white oaks, and the live oaks, there exist both short and tall species. This trait also showed very high similarity within communities. A number of other traits were examined in a previous study (Cavender-Bares et al. 2004a) and are indicated with small, open circles in Fig. 3B. Relatively convergent traits from this analysis included maximum hydraulic conductivity, whole-shoot transpiration rate, vulnerability to cavitation during drought, absolute and relative growth rates, ability to resprout from rhizomes, and bark thickness. At the same time, traits that were fairly conserved tended to show overdispersion (or low

similarity within communities), such as seed mass and specific leaf area (particularly for shade leaves), or wood density, acorn maturation time, and leaf lifespan from the previous analysis. In both the present study and the previous analysis, there was a remarkable absence of conserved traits that showed clustering (or high similarity) within communities. This contrasts sharply with the pattern seen for all woody plants (Fig. 3A). For the oaks, trait similarity was highest for convergent traits and lowest for conserved traits. These results indicate that the pattern of phylogenetic overdispersion in oak communities is generated by the combination of environmental filtering of convergent traits and overdispersion of conserved traits.

DISCUSSION

It has long been recognized that plants can show a high degree of evolutionary stasis (e.g., Li 1952, Wen 1999, Qian and Ricklefs 2004) and niche conservatism (Webb et al. 2002, Ackerly 2003, Reich et al. 2003). At the same time, evolutionary processes that cause differentiation of sister taxa, such as character displacement

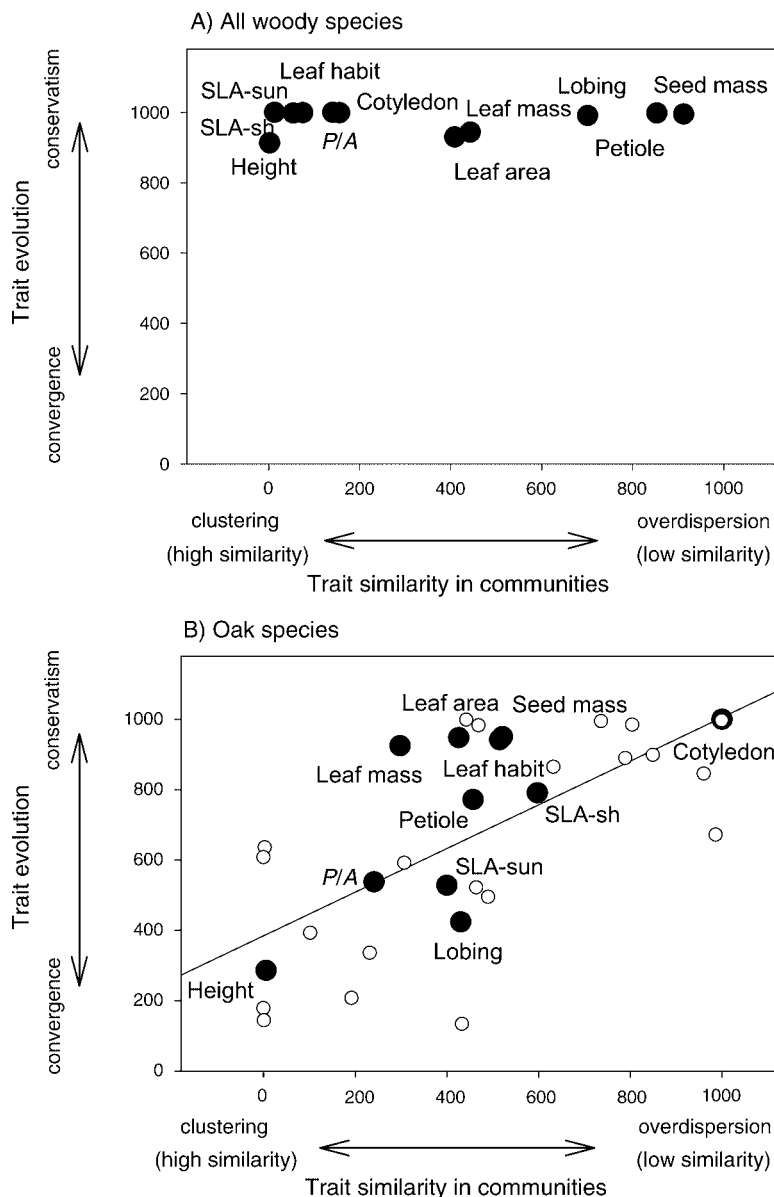A) All woody species

B) Oak species

FIG. 3. Conservatism of traits in relation to trait similarity within communities for (A) all woody species and (B) oak species only. Traits are ordered on the x- and y-axes by the ranking of the observed similarity or phylogenetic signal of each trait relative to 999 simulations in the null model (the ranking of the r values of observed data for trait similarity relative to simulated data increases with overdispersion [vs. clustering], and the ranking of the observed phylogenetic signal relative to simulated data decreases with conservatism [vs. convergence]). Traits include the following (labeled solid circles): leaf area, specific leaf area (SLA)-sun, SLA-shade (SLA-sh), perimeter-to-area ratio (P/A), leaf habit, leaf mass, lobing, petiole length, cotyledon type, seed mass, and height. Open circles represent a suite of other morphological, physiological, and life history traits, measured from trees in the field as well as from seedlings in a common garden from a previous study (Cavender-Bares et al. 2004). The contrasting patterns of trait evolution and community similarity for the whole woody plant community and the oak lineage help explain the contrasting phylogenetic structures of communities observed at these different taxonomic scales.

(e.g., Schluter 2000) and adaptive radiation (e.g., Givnish et al. 2000) are well documented. To the extent that evolutionary stasis predominates, close relatives are likely to occur in similar habitats, given that plants will track environments for which they are adapted (Ackerly 2003). The principle of competitive exclusion presents a paradox, however, because close relatives that are too similar cannot coexist (e.g., Elton 1946, MacArthur and Levins 1967, Chesson 2000). In this study, we suggest a solution for this paradox by showing that plant communities can simultaneously exhibit niche conservatism and overdispersion of close relatives. The signal that dominates depends on the scale at which communities and the taxa in them are examined.
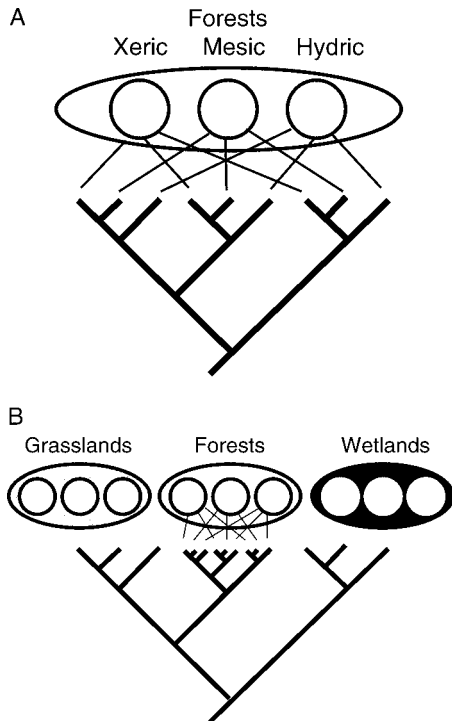
FIG. 4. The phylogenetic structure of communities is dependent on the scale at which they are defined. Apparent overdispersion within forest communities (A), for example, can appear as clustering when grassland and wetland communities are included (B). At the same time, phylogenetic structure also depends on the phylogenetic scale or taxonomic inclusiveness. Apparent overdispersion within a lineage is more likely to appear as a dominant pattern of clustering when the analysis includes many lineages.

Phylogenetic structure of communities at different spatial and taxonomic scales

Both the spatial scale and resolution of species abundance data influence the observed phylogenetic structure in community assemblages. Greater overdispersion is detected at smaller spatial scales and with higher resolution data. This is demonstrated by more significant overdispersion when using basal area within plots rather than presence/absence (Table 1). Basal area provides higher resolution for species distributions, and the extent to which they overlap within communities, and hence could provide more precision for detecting overdispersion. The difference in null model is apparently not a factor in this outcome, as the same results were found using null model 3 (randomization of the phylogeny instead of the communities; Table 1). Phylogenetic overdispersion is more easily detected among close relatives when the communities included in the analysis are limited to only those in which the focal lineage occurs (Table 1). This effectively reduces the spatial area and environmental heterogeneity examined. These results make clear that phylogenetic overdispersion can occur at small spatial scales, even while

clustering occurs at larger spatial scales when a greater range of community types is included (Fig. 4).

The phylogenetic structure of communities depends even more strikingly on the phylogenetic scale, or inclusiveness of taxa. Communities within a region may appear overdispersed at one phylogenetic scale (e.g., within one lineage), but clustered at a broader phylogenetic scale (e.g., when including all seed plants in the community). This allows a reconciliation of apparently contradictory results, as both niche conservatism and species interactions are important forces in community assembly, but are dominant at different scales. Species interactions that give rise to phylogenetic overdispersion show a stronger signal when communities are delimited to include a single monophyletic lineage. Niche conservatism shows a stronger signal the more broadly a community is defined taxonomically. Speciose lineages, such as the oaks, may be more likely to show overdispersion than less speciose lineages if, for example, increased diversity leads to increased competition among closely related species. Phylogenetic patterns are also likely to be lineage-specific, and it is not known the extent to which the oaks represent an exceptional scenario. Hence, the specific results found here might not be generalizable to other systems (see, for example, Kembel and Hubbell 2006). Nevertheless, the study does demonstrate the potential of phylogenetic patterns to vary predictably with scale and demonstrates that both phylogenetic overdispersion and clustering can occur at different spatial and taxonomic scales in the same study system.

Phylogenetic structure within single lineage communities

Phylogenetic dispersion patterns of species in communities that are narrowly defined taxonomically appear to be lineage specific, and may depend on intrinsic properties of lineages, biogeographic history, and lineage diversity. One possibility is that phylogenetic overdispersion might be more likely in speciose lineages due to intensification of species interactions. In addition, overdispersion might be more likely in lineages that have undergone adaptive radiations more or less in situ, as the evolutionary process should result in close relatives occupying different habitats as well as high local diversity. The American oaks are a likely example of such a radiation. Oaks are believed to have reached the Americas from Eurasia ~40 million years ago and are subsequently thought to have undergone a rapid radiation with all of the major subgenera appearing in the fossil record by 35 million years ago (Crepet and Nixon 1989). Many of the southeastern oaks are endemic to the region, and biogeographic evidence suggests that diversification of the oaks in the Americas occurred in their current localities (Manos et al. 1999, Manos and Stanford 2001). The Florida peninsula was not connected with North America and was submerged under the ocean until 20 million years ago (Webb 1990). The colonization of Florida, therefore, occurred subsequent to this time period. Fossil records indicate that

the flora was originally tropical, but increasingly invaded by deciduous hammock communities, similar to those of today, starting about 17 million years ago as the climate cooled. The availability of new habitats for colonization might have facilitated rapid adaptation, possibly aided by promiscuous exchange of genetic material among species. The present-day overdispersion of oaks (Table 1; Mohler 1990, Cavender-Bares et al. 2004a) could thus be the result of their evolutionary history of adaptive radiation into novel habitats.

The hollies show some degree of overdispersion (Fig. 3C) under null model 2, although this pattern is not significant under null model 3, and hence the signal is somewhat ambiguous. *Ilex* diversified in the Eocene, ~50 million years ago and was already dispersed over all of the major continents by that time (Cuenoud et al. 2000). These small-seeded, bird-dispersed species arrived in Florida over the course of the past 20 million years, but for the most part evolved before then on other continents in other contexts. With the exception of two pairs, *Ilex cassine* and *Ilex myrtifolia*, and *Ilex decidua* and *Ilex ambigua*, speciation did not occur in the context of the other hollies that currently inhabit Florida, and currently sympatric congeners could have large intervening branch length distances (Cuenoud et al. 2000). The lack of co-occurrence between the closely related members in each pair gives rise to the apparent trend of overdispersion under null model 2 (Fig. 3C). The relatively weak signal, however, might result from a very different biogeographic history of the hollies or, alternatively, from the fact that the hollies are much less speciose than the oaks, particularly in this study region.

The pines show a hump-shaped phylogenetic pattern, in which only pines of intermediate relatedness co-occur (Fig. 3D). It has previously been noted for the pines in Florida that sister species do not co-occur and that co-occurring species are not closely related (Adams and Jackson 1997). Hence, some degree of phylogenetic overdispersion has been observed within the genus, even though we did not detect it in north central Florida. The lack of clear phylogenetic signal in pine communities might result from the lower diversity of the pines relative to the oaks, causing congeneric competition to be less important among the pines.

The strong signal of overdispersion in the oaks might result from their history of adaptive radiation and their high local diversity. Additional studies are needed to determine (1) the extent to which overdispersion among close relatives depends on historical and lineage-specific factors and (2) the extent to which local diversity within lineages might influence the intensity of species interactions that give rise to phylogenetic overdispersion in communities.

Trait evolution and community assembly

Nonneutral ecological processes that influence community assembly act on the phenotypes of species. Therefore, the phylogenetic structure of communities ultimately depends on (1) the evolutionary history of species' traits and (2) the extent to which traits influence species distributions across environmental gradients or prevent coexistence due to species interactions. Closely related species are likely to co-occur if traits important for environmental filtering are conserved. On the other hand, if traits important for environmental filtering are convergent, or many different strategies for existing in a given habitat are possible, then closely related species might not co-occur. Likewise, if similarity in particular traits prevent coexistence, and such traits are conserved, then closely related species are again unlikely to co-occur.

Of course, if species distributions are not related to their phenotypes, as predicted by neutral models (Hubbell 2001), then phylogenetic patterns in community structure are unlikely to emerge (Kembel and Hubbell 2006). However, lack of clear phylogenetic patterns might also result from species interactions and environmental filtering operating in opposing directions. In this study, for example, phylogenetic overdispersion of oaks apparently masks the pattern of phylogenetic clustering that predominates among angiosperm lineages. When oaks are removed from the analysis, the clustering pattern becomes apparent (Table 1).

Among species in the broadly defined Floridian communities, all traits examined showed a fairly high degree of conservatism (Fig. 3A). A subset of these traits showed high similarity within communities (clustering), including specific leaf area for both sun and shade leaves, leaf habit, maximum height, leaf perimeter-to-area ratio, and cotyledon type. These traits have generally been shown to be important in the ability of species to respond to abiotic stress factors and to influence species distributions across environmental gradients, critical evidence for their potential role in environmental filtering. For example, specific leaf area and leaf habit, a proxy for leaf lifespan, are both important in the carbon economy of plants (e.g., Kikuzawa 1991, Damesin et al. 1998, Kikuzawa and Ackerly 1999) and have been well documented to vary with soil nutrient availability at various spatial scales (Monk 1966, Reich et al. 1999, Wright et al. 2002, Reich et al. 2003). Specific leaf area is also likely to be associated with canopy openness and soil moisture availability (Wright et al. 2002). Maximum height has been linked to growth rate (Thomas 1996), and taller height is a competitive strategy for accessing light in productive environments (Tilman 1988). In lower productivity environments or in communities prone to burning, less investment in aboveground biomass is expected (Schwilk and Ackerly 2001, Cavender-Bares et al. 2004b). Leaf perimeter-to-area ratio has been correlated to hydraulic conductance (Sack et al. 2003) and is likely to be important in distribution patterns across soil moisture gradients (Brodribb and Holbrook 2003). The primary role of cotyledons as either storage organs or photosynthetic organs represents a trade-off in regeneration strategies that depend on resource

availability (Kitajima and Fenner 2000). The previously established linkages to resource capture and use for all of the traits that show high similarity (clustering) within communities support the interpretation that these traits are likely to be important for habitat tracking and environmental filtering. Clustering of conserved traits is critical in explaining the emergent pattern of phylogenetic clustering in Floridian plant communities.

Other traits, including leaf mass, leaf area, lobedness, petiole length, and seed mass showed low similarity within communities. These traits might be less adaptive to environmental factors, or at least to those that vary at the same scale as the plot survey, and might be associated with architectural constraints. Alternatively, there could be multiple trait strategies that are successful in a given community. For example, leaf size and leaf lobing have been linked to boundary layer conductance and heat load (Givnish 1976), which could be important in environmental filtering. However, various combinations of leaf size, shape, leaf angle, leaf display, and pubescence can achieve a similar energy balance (Lambers et al. 1998, Ackerly 1999). Leaf size, seed size, and petiole length might also be more related to plant architecture than to external environmental gradients (e.g., Mazer 1989, Lord et al. 1995, Moles et al. 2005), and these traits have not generally shown strong trait–environment correlations.

While all the traits measured in this study were fairly conserved in the broad analysis, many of the same traits tended to be convergent, or not different from random expectation, within the oak genus (Fig. 3B). For example, maximum height, the perimeter-to-area relationship, and specific leaf area were more convergent within the oaks than among the larger species pool. This result is not surprising if trait variance among lineages is higher than the variance within a lineage (Felsenstein 1985, Harvey and Pagel 1991). In other words, even if sister taxa show divergent morphology, recent common ancestry of closely related species is likely to limit the amount of divergence within a lineage, relative to that found among distantly related lineages. This could explain the shift to conservatism at broader taxonomic scales. Specific leaf area, a fairly labile trait within the oaks, for example, varied roughly threefold within the genus, but exceeded fivefold among all species sampled. However, in a study of almost 13 000 seed plants, Moles et al. (2005) showed that higher divergences sometimes occurred within a family than between families. A number of genera, particularly speciose genera in which many members co-occur, have also been shown to have divergences within them equal to or greater than those between co-occurring species that are distantly related (Silvertown et al. 2006). Therefore, the shift toward trait conservatism at the broader phylogenetic scale can also be explained as a result of swamping out the signal of high trait lability within the oaks by the addition of many more taxa that have conserved traits. Maximum height, for example, shows as much variation within the

oaks (~60-fold difference) as it does across all species examined at the broader scale, but this level of variation within a clade is unique to the oaks in our study. The shift in patterns of trait evolution toward increasing conservatism at broader taxonomic scales is likely to explain the concomitant shift in the phylogenetic structure of communities toward clustering. It also lends support to the view that niche conservatism is widespread among plants (Wen 1999, Webb et al. 2002, Ackerly 2003, Qian and Ricklefs 2004).

The oaks, which dominate many woody communities in north central Florida, appear to represent a special case in this study system. They show an unusual amount of lability in certain functional traits, such as maximum height, water transport capacity, growth rate, and the ability to resprout from rhizomes (Cavender-Bares et al. 2004a), traits important for habitat specialization (Cavender-Bares et al. 2004b). The observed phylogenetic overdispersion among the Floridian oaks could be a result of their history of adaptive radiation and might be maintained by reduced competition among co-occurring species of different subgenera or lower density-dependent mortality (Cavender-Bares et al. 2004a). The latter possibility has been hypothesized as a result of pathogen specificity at taxonomic levels above the species (Janzen 1970, Webb and Gilbert 2006). At larger taxonomic and spatial scales, however, Floridian plant communities show phylogenetic clustering. This can be accounted for by conservatism of functional traits that influence species distributions. These contrasting patterns that emerge within the same study system illustrate the importance of scale in detecting opposing ecological and evolutionary forces.

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APPENDIX A

Species used in each analysis (*Ecological Archives* E087-114-A1).

APPENDIX B

References for phylogenetic data (*Ecological Archives* E087-114-A2).

APPENDIX C

Phylogenetic trees used in each analysis (*Ecological Archives* E087-114-A3).