The role of diversification in community assembly of the oaks (*Quercus* L.) across the continental U.S.

Jeannine Cavender-Bares[1,7], Shan Kothari[2,7], José Eduardo Meireles[1,7], Matthew A. Kaproth[1,4], Paul S Manos[3], and Andrew L. Hipp[5,6]

[1] Department of Ecology, Evolution and Behavior, University of Minnesota, 1479 Gortner Avenue, St. Paul, MN 55108, USA

[2] Department of Plant Biology, University of Minnesota, 1479 Gortner Ave, St. Paul, MN 55108, USA

[3] Department of Biology, Duke University, Durham, NC 27708, USA

[4] Department of Biological Sciences, Minnesota State University, Mankato, MN 56001, USA

[5] The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532, USA

[6] The Field Museum, 1400 S Lake Shore Drive, Chicago, IL 60605, USA

[7] Authors for correspondence (e-mails: cavender@umn.edu, kotha020@umn.edu, meireles@umn.edu)

PREMISE OF THE STUDY: Evolutionary and biogeographic history, including past environmental change and diversification processes, are likely to have influenced the expansion, migration, and extinction of populations, creating evolutionary legacy effects that influence regional species pools and the composition of communities. We consider the consequences of the diversification process in shaping trait evolution and assembly of oak-dominated communities throughout the continental United States (U.S.).

METHODS: Within the U.S. oaks, we tested for phylogenetic and functional trait patterns at different spatial scales, taking advantage of a dated phylogenomic analysis of American oaks and the U.S. Forest Service (USFS) Forest Inventory and Analysis (FIA).

KEY RESULTS: We find (1) phylogenetic overdispersion at small grain sizes throughout the U.S. across all spatial extents and (2) a shift from overdispersion to clustering with increasing grain sizes. Leaf traits have evolved in a convergent manner, and these traits are clustered in communities at all spatial scales, except in the far west, where species with contrasting leaf types co-occur.

CONCLUSIONS: Our results support the hypotheses that (1) interspecific interactions were important in parallel adaptive radiation of the genus into a range of habitats across the continent and (2) that the diversification process is a critical driver of community assembly. Functional convergence of complementary species from distinct clades adapted to the same local habitats is a likely mechanism that allows distantly related species to coexist. Our findings contribute to an explanation of the long-term maintenance of high oak diversity and the dominance of the oak genus in North America.

  KEY WORDS   community assembly; complementarity; convergent evolution; diversification processes; environmental sorting; evolutionary legacy effects; functional traits; phylogenetic structure; species interactions; sympatric parallel adaptive radiation.

The integration of phylogenetic biology and functional ecology into the study of biological communities has helped in deciphering the processes that shape community assembly (Webb et al., 2002; Kraft et al., 2007; Vamosi and Vamosi, 2007; Cavender-Bares et al., 2009; Kraft and Ackerly, 2010; Eaton et al., 2012; Hawkins et al., 2014). These advances are critical to understanding the predictability of ecosystem composition under global change and highly relevant

to ecosystem restoration in the face of widespread anthropogenic disturbance (Cavender-Bares and Cavender, 2011; Hipp et al., 2015; Barak et al., 2016). While competitive interactions and environmental sorting processes have been highlighted as critical to local community assembly (Weiher and Keddy, 1999a; Webb et al., 2002), diversification and long-term evolutionary and biogeographic processes remain underappreciated in understanding local

community assembly (Gerhold et al., 2015). The role of historical processes in the assembly of plant communities remain understudied, despite the known importance of adaptive radiation and historical colonization patterns in the assembly of island and continental floras (Pennington et al., 2004, 2009; Ricklefs, 2004; Emerson and Gillespie, 2008; Crisp et al., 2009; Fine, 2015). Here we examine the functional and phylogenetic structure of oak-dominated tree communities from local to continental scales to examine the consequences of evolutionary and historical processes in shaping the composition and diversity of North American oak forest communities. Our goal is to link deep-time processes to current patterns in an effort to understand why the oaks have unusually high local and continental diversity and abundance.

The phylogenetic structure of co-occurrence patterns is a cumulative consequence of historical processes, such as speciation, extinction, and dispersal (Kembel, 2009; Villalobos et al., 2013), ecological interactions and genetic processes, such as disease (Gilbert and Webb, 2007) and pest (Mouillot et al., 2005; Lind et al., 2015) dynamics, introgression (Eaton et al., 2015; Pollock et al., 2015), competition (Davies et al., 2007; Cooper et al., 2008), facilitation (Valiente-Banuet and Verdú, 2007), and environmental sorting (Helmus, 2007; Savage and Cavender-Bares, 2012; Swenson et al., 2012) (Box 1). Over long timescales, ecological processes and introgression surely influence evolutionary dynamics and diversification, shaping the radiations of important lineages and their ongoing community assembly processes (Van Valen, 1976; Schluter, 2000; Ricklefs, 2007; Tyerman et al., 2008; Givnish et al., 2009; Keller et al., 2013; Cannon and Lerdau, 2015). Historical diversification processes have also influenced the evolution of functional traits, thus influencing the extent to which closely related species are adapted to similar or contrasting habitats. At shorter timescales, density-dependent ecological processes and environmental selection pressures drive the co-occurrence patterns and sorting of species into habitats. Yet the functional traits of organisms that are mechanistically linked to these processes reflect their longer-term evolutionary history.

A persistent challenge is to tease apart the influence of multiple processes interacting in complex ways to shape the structure of species assemblages (Lessard et al., 2015), given that there are more potential processes that may account for the structure of species assemblages than there are resulting patterns (Wainwright et al., 2005; Cavender-Bares et al., 2009; Mayfield and Levine, 2010; Gerhold et al., 2015). As a consequence, similar patterns can emerge from very different processes. For example, introgression of two close relatives can cause them to merge into a single species, resulting in the same expected community pattern as competitive exclusion, whereby one species excludes another (Levin, 2006; Pollock et al., 2015). In both cases, close relatives would not be observed to occur in the same community (Cavender-Bares et al. 2009). The processes that drive species distributions and diversity patterns may have counterintuitive impacts on phenotypic and phylogenetic dispersion of co-occurring species (Prinzing et al., 2008; Mayfield and Levine, 2010). While trait differences may enhance resource complementarity (Kraft et al., 2008), the strength and outcome of competitive interactions are not necessarily predicted by similarity or dissimilarity (Kraft et al., 2015b), and competitive outcomes may be driven by trait hierarchies, such that dissimilarity could lead to competitive exclusion (Kunstler et al., 2012; Lasky et al., 2014). Hierarchical interactions would be expected if more acquisitive trait values are advantageous in resource-rich environments, or if

resource-conservative trait values are advantageous in resource-limited environments (Chabot and Hicks, 1982; Kikuzawa, 1995; Reich, 2014). Furthermore, biotic interactions involving facilitation are frequently overlooked in hypothesized consequences of species interactions for community structure (Valiente-Banuet and Verdú, 2007). While phylogenetic overdispersion is frequently attributed to competitive exclusion or other density-dependent processes under the umbrella of biotic interactions, both empirical and simulation studies have shown that it can be caused by habitat sorting processes and environmental filtering if critical functional traits that influence distributions are convergent (Cavender-Bares et al., 2004b; Kraft et al., 2007). Understanding why traits may be convergent ultimately requires knowledge of diversification.

The processes that dominate community assembly vary with spatial scale (Weiher and Keddy, 1999b; Laliberté et al., 2009) and thus lead to shifting expectations of phylogenetic and trait structure in communities (Cavender-Bares et al., 2006; Swenson et al., 2006, 2007; Willis et al., 2010; Brunbjerg et al., 2014; Yan et al., 2016). Grain size and spatial extent are two distinct but important components of spatial scale (Turner et al., 2001) that are expected to have different consequences for community structure. A community assemblage is defined by the grain size (i.e., the plot size of an observed assemblage) that we choose, while comparisons among assemblages and the pool of species that we assume those assemblages are derived from depend on the spatial extent that we circumscribe for the analysis. At small grain sizes, our focal species can be assumed to interact (or potentially interact) directly, and environmental conditions may be relatively homogeneous, whereas at increasing grain sizes individuals within the assemblage would be less likely to interact directly, although environmental variation may increase among assemblages, depending on the scale of variation of the most critical environment axis. Keddy and Weiher (1999) thus hypothesized that biotic interactions should have greater importance at smaller spatial scales, whereas environmental adversity should influence assembly more strongly at larger spatial scales.

Phylogenetic similarity can be used proximally as an integrated measure of functional similarity and can stand in for unmeasured traits (Cadotte et al., 2009, 2011). Phylogenetic similarity is compellingly linked to similarity in susceptibility to disease (Webb et al., 2006; Gilbert and Webb, 2007) and to increasing potential for introgression due to incomplete reproductive isolation (Levin, 2006; Cavender-Bares et al., 2009; Larcombe et al., 2015; Pollock et al., 2015). Yet, individual ecophysiological traits relevant to specific community assembly mechanisms are frequently labile within or across focal lineages (Losos et al., 2003; Savage and Cavender-Bares, 2012). In close proximity (assemblages measured at small grain sizes), close relatives may be predicted to co-occur less frequently than at random if biotic interactions prevent co-occurrence among organisms with similar niches or with similar vulnerabilities to pests and pathogens. Predicting competitive outcomes of functionally or phylogenetically similar species is fairly complex, as is predicting the consequences of dispersal differences (Tilman, 1994; Kembel, 2009; Mayfield and Levine, 2010). However, we do expect functionally similar species to acquire resources similarly (Lebrija-Trejos et al., 2010; Reich, 2014), to have similar environmental tolerances (Ackerly, 2003; Cavender-Bares et al., 2004a; Niinemets and Valladares, 2006; Baraloto et al., 2007) and to have fitness advantages in similar environments (Wei et al., 2017), such that they co-occur in similar environments more frequently than at random (Kraft et al., 2015b). With increasing grain sizes, we expect

Box 1 Phylogenetic and trait structure of communities: hypotheses and considerations

Community assembly is influenced by multiple processes, which we categorize here in terms of (1) direct interactions among focal species in the community or density-dependent interactions mediated by unobserved organisms, such as pests and pathogens, (2) interactions of species with their environment, particularly the critical environmental gradients that influence their distributions, given species' physiological tolerances, (3) long-term dispersal processes that influence how circumscribed species and lineages are geographically distributed and (4) historical diversification processes that generated the species pool from which local communities are assembled. Each of these factors (and others not considered) plays a role in driving patterns that emerge in extant communities.

The diversification process tends to be underemphasized in deciphering processes involved in community assembly that generate current patterns of composition and diversity. Contrasting phylogenetic and trait dispersion patterns should arise in communities comprised of relatives of the same clade as a consequence of whether speciation can be attributed to (1) a classic allopatric speciation model in which species within a clade have evolved to span major environmental gradients (Box 1: Fig. 1A) or (2) a sympatric parallel adaptive radiation, in which major clades within a lineage have simultaneously radiated to fill the same ecological niches (Box 1: Fig. 1B), as in the case of the American oaks (Hipp et al., 2018). In the case of allopatric diversification, functional traits that correspond to species' ecological niches are likely to be phylogenetically conserved (Box 1: Fig. 1A), such that functional trait distances and phylogenetic distances between species correspond. In the case of sympatric parallel diversification, members of distinct clades will share the same ecological niches as a consequence of convergent evolution (Box 1: Fig. 1B). Convergence between major clades may occur even though within each clade functional traits and niches may be phylogenetically conserved, at least for some niche axes. Regardless, convergence between clades will cause functional trait distances to be uncoupled from phylogenetic distances among species. All else equal, diversification history would lead to an expectation of phylogenetic clustering in the case of allopatric diversification (Box 1: Fig. 1C) and overdispersion in the case of sympatric parallel diversification (Box 1: Fig. 1D).

Species interactions contribute to short-term co-occurrence patterns and determine long-term coexistence. Coexistence, or its absence, of species within lineages is not just a function of competition. Lack of sufficient reproductive isolating mechanisms may prevent populations of closely related species from maintaining coherence, and spatial proximity of close relatives likely contributes to density-dependent mortality as a consequence of Janzen–Connell type mechanisms (Gilbert and Webb, 2007). These factors may prevent coexistence of closest relatives, leading to an expectation of phylogenetic overdispersion in local communities (Box 1: Fig. 1E, F). As other authors have pointed out, species that persist within communities must be similar enough to persist in the same environment but different enough to allow coexistence (Mayfield and Levine, 2010). Functional traits that influence sorting processes along environmental gradients (ecophysiological traits associated with environmental tolerances) may be uncoupled from those that influence reproductive isolating mechanisms and vulnerability to enemies (reproductive incompatibility or defense and immunity traits). As a consequence, regardless of diversification history, ecophysiological traits are likely to be clustered within communities to the extent that individuals experience similar environments within the spatial bounds of the community (Box 1: Fig. 1G, H). Trait clustering may become stronger with larger grain size because fewer species interact directly, dampening the effects of those interactions (Box 1: Fig. 1E, F), particularly if environmental gradients become steeper with distance (Box 1: Fig. 1G, H).

Functional traits that influence reproductive isolation or response to natural enemies have frequently been observed to show phylogenetic conservatism (e.g., Webb et al., 2006; Gilbert and Webb, 2007), whereas traits determining physiological tolerance across gradients may show convergence, particularly in cases where sympatric parallel adaptive radiation has occurred (Kozak et al., 2009). Therefore, under an allopatric diversification model, the trait structure of organisms within communities may be expected to follow the phylogenetic structure. However, under a sympatric parallel adaptive radiation model, functional traits related to environmental niches would be expected to converge between major lineages. In contrast, reproductive isolating mechanisms or vulnerability to enemies may nevertheless be phylogenetically conserved.

The dominant processes that structure communities are likely to change as the size of the community shifts from a small grain size, in which all individuals within it are able to interact, to a large grain size in which most individuals within the community likely do not interact directly but share a similar environment or at least some aspects of the environment. At local scales, the importance of species interactions may pose barriers to the coexistence of close relatives, while at larger grain sizes the importance of species interactions is relaxed. This is true for both speciation models.

In the allopatric diversification model, species only need to be distantly related enough to avoid exclusion, but their degree of difference may be quite similar to what would be expected in the case of random draws from the phylogeny, assuming the null model applies a large spatial extent and pool size. Matching of traits to the environment is important at all spatial scales. However, its consequences for phylogenetic and trait structure may be counterbalanced by species interactions at small grain sizes but not at larger grain sizes, resulting in phylogenetic and trait clustering at larger scales. We might thus anticipate a shift from random dispersion to phylogenetic and trait clustering with increasing grain sizes (Box 1: Fig. 2B, D).
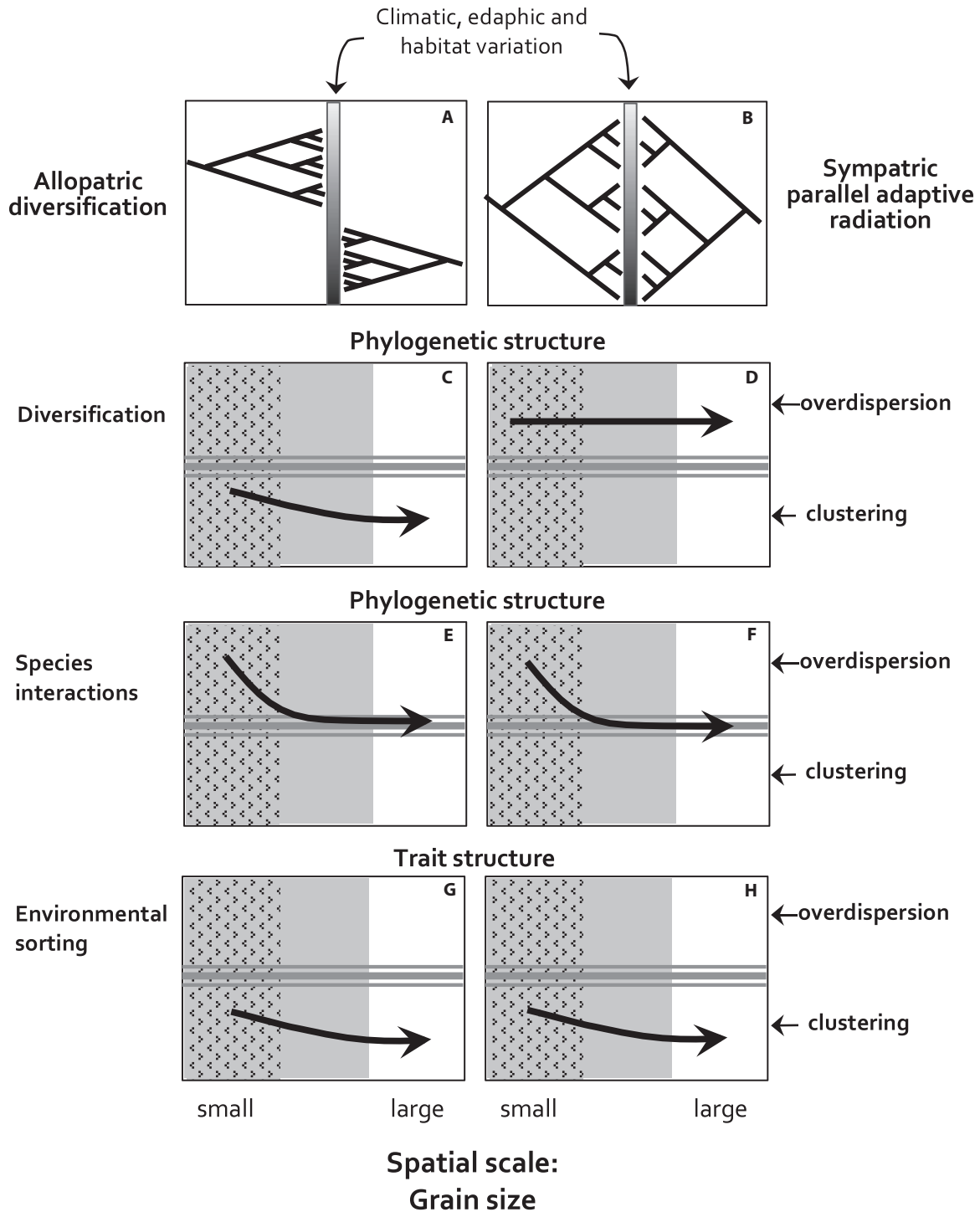
When grain size is held constant while spatial extent of the analysis increases, the phylogenetic representation is increased as well as the size of the pool from which communities are locally assembled. While the pairwise phylogenetic and trait distances of species in these small communities should stay the same, their *expected* distances based on the changing species pool may change. In the allopatric case, increasing the spatial extent will increase the expected distances between co-occurring species under the null model, potentially shifting patterns of phylogenetic and trait overdispersion to randomly dispersed patterns in which observed communities do not differ from randomly simulated communities or in which observed communities are more clustered than

Box 1 (continued)

simulated ones (Box 1: Fig. 2C, E). A contrasting situation emerges in the case of sympatric parallel diversification. In local communities of constant grain size, phylogenetic distances between co-occurring species are expected to be high, since members of distantly related clades are sympatric. With increasing spatial extent a larger portion of each of the major clades is encompassed, potentially decreasing the expected distance in simulated communities or at least not increasing it, if additional species are intermediately related.

Based on this set of considerations and assumptions, we generate a series of hypotheses for how the nature of the diversification process—for example, allopatric diversification along environmental gradients (Box 1: Fig. 2A) or sympatric parallel diversification along
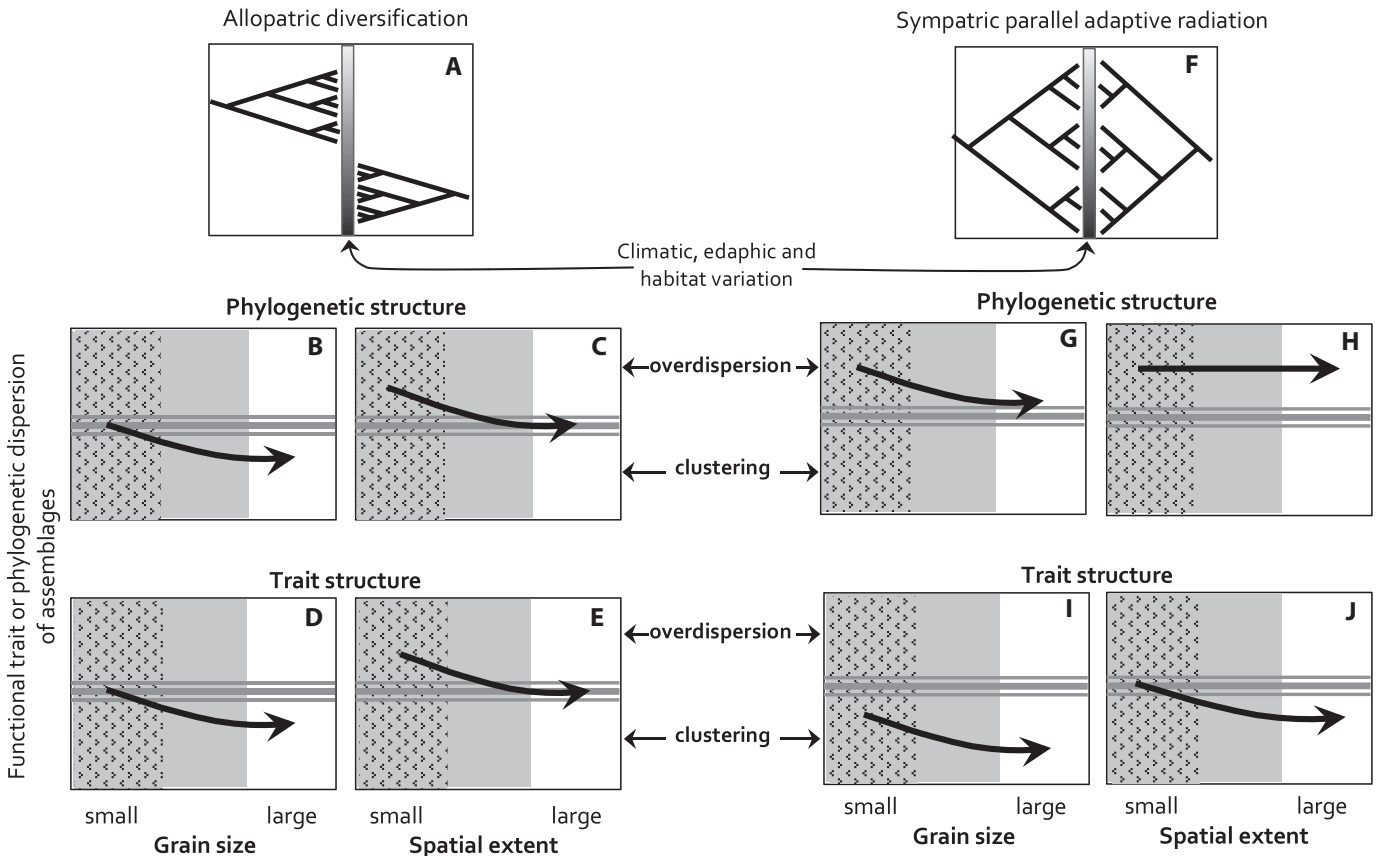
BOX 1: FIGURE 1

Box 1 (continued)

environmental gradients (Box 1: Fig. 2F)—in concert with the relative importance of interspecific interactions, environmental sorting, and long-term dispersal limitation, influence the phylogenetic and functional trait dispersion of communities as grain size (Box 1: Fig. 2B, D, G, I) and spatial extent (Box 1: Fig. 2C, E, H, J) increase from small to large. Environmental variation is depicted by the shaded gradient bar in the center (Box 1: Fig. 2A, F). While many potential diversification scenarios can be imagined, only two cases are shown in the left and right panels, respectively.

In the left panels, we assume a classic pattern of allopatric diversification along climatic, edaphic, and topographic gradients. Species interactions should be most direct and intense at small grain sizes. Certain kinds of species interactions, such as enemy-mediated mortality, are hypothesized to prevent coexistence of close relatives and to result in phylogenetic overdispersion if close relatives share susceptibility to the same enemies. Trait dispersion patterns should follow suit, given that traits are expected to be phylogenetically conserved. At intermediate and large spatial scales (grain sizes), as climatic, edaphic, and topographic variation among communities become more pronounced, species interactions are expected to relax, and sorting based on matching between ecophysiological traits and the abiotic environment may become more important. Ecological sorting may cause trait clustering and, thus, phylogenetic clustering (assuming trait conservatism). Moreover, the geography of speciation, whereby a lineage diversifies in a given region and members of that lineage are circumscribed geographically due to long-term dispersal limitation, can result in phylogenetic clustering at large grain sizes (Box 1: Fig. 2B). When grain size is held constant at a small plot size but spatial extent is increased, expanding the phylogenetic breadth of the pool from which species in communities can potentially be assembled, phylogenetic and trait structure shifts from over-dispersion to a pattern indistinguishable from random expectation (Box 1: Fig. 2C).

In the right panels, we assume diversification occurred sympatrically and in parallel along environmental gradients (Box 1: Fig. 2F). Given the nature of diversification, traits are likely to be convergent in distantly related species occupying the same habitats. Phylogenetic overdispersion is expected at small grain sizes (Box 1: Fig. 2G) at all spatial extents (Box 1: Fig. 2H) but should tend toward randomness at larger grain sizes, when spatial extent is held constant and is large (Box 1: Fig. 2D). In contrast, traits important for environmental sorting are expected to cluster at all grain sizes, but may show increased clustering if larger grain sizes are associated with steeper environmental gradients (Box 1: Fig. 2I). At small grain size and small spatial extent, in which there is little environmental heterogeneity, trait structure should not be different from random expectation. To the extent the traits measured are important for complementarity in resource use, they may be overdispersed (not shown). With increasing spatial extent (Box 1: Fig. 2J), however, greater environmental heterogeneity is likely encompassed, and traits should again become increasingly clustered.
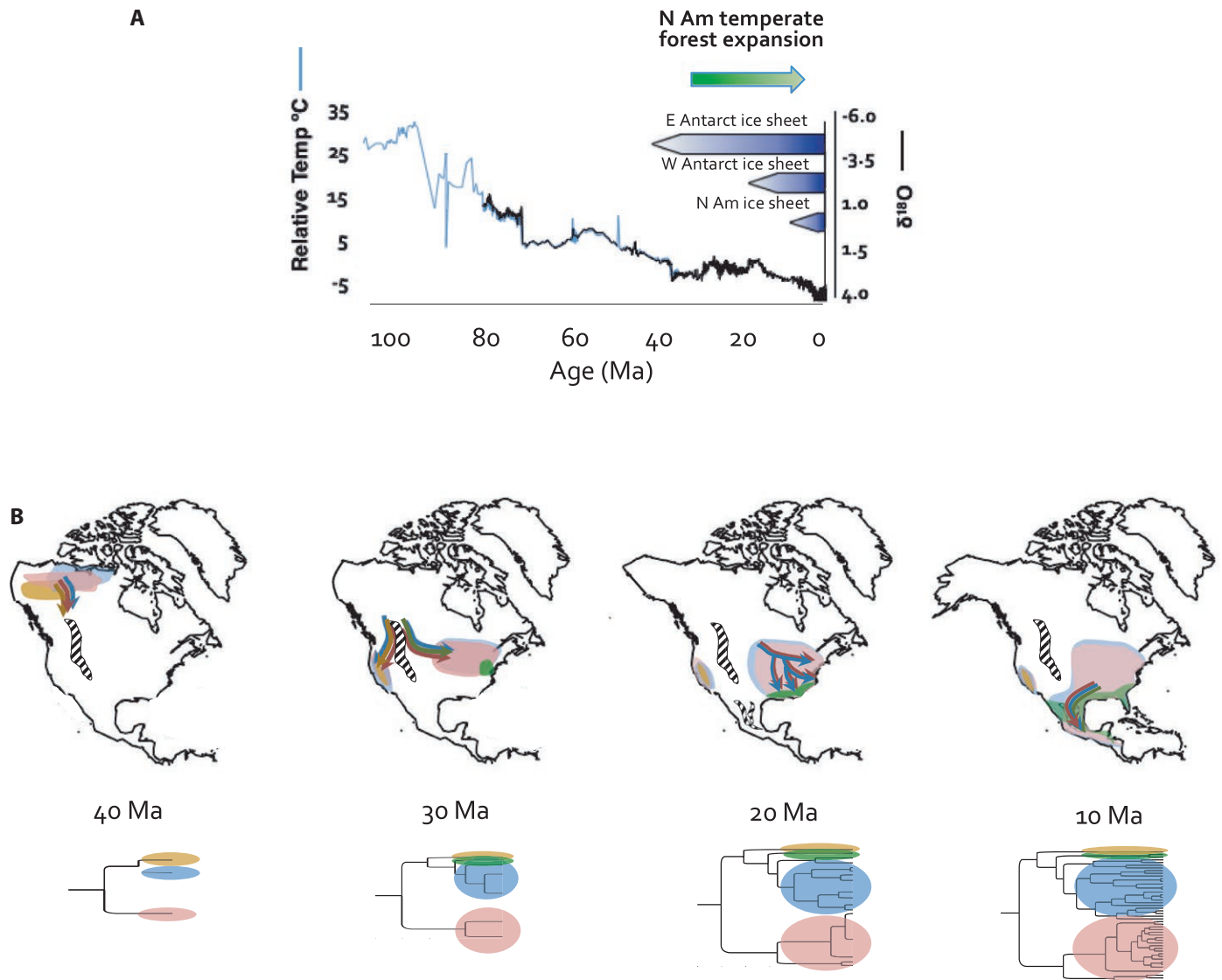
BOX 1: FIGURE 2

FIGURE 1. (A) Declining global sea surface temperature temperatures in the Paleogene based on [18]O sediment records (Zachos et al., 2001; Forster et al., 2007; Alsenz et al., 2013; Van Der Meer et al., 2014; Thibault et al., 2015) in relation to the geologic time line, showing formation of major ice sheets as Earth cooled and expansion of the North American temperature forest biome. (B) Schematic showing pattern of colonization, expansion, and diversification of the major oak lineages in North America, following Hipp et al 2018. Both red oaks (section *Lobatae*, rose color) and white oaks (section *Quercus,* blue color) expanded and radiated in parallel. Section *Protobalanus* is shown in gold, section *Virentes* in green. Oaks were initially at high latitudes, descended to middle latitudes, splitting east and west, diversifying in the east and subsequently colonizing Mesoamerica.

the strength of direct interactions among species to fade (Box 1: Fig. 1E, F), but not environmental sorting processes, likely resulting in increasing trait clustering (Box 1: Fig. 1G, H). To the extent that phylogenetic similarity reflects functional similarity relevant to environmental sorting, we also expect an increase in phylogenetic clustering (Box 1: Fig. 2B).

With increasing spatial scale, particularly at the scale of biomes, we expect long-term dispersal limits and environmentally constrained diversification to influence the phylogenetic structure of the biota (Losos and Glor, 2003; Gerhold et al., 2015; Souza-Neto et al., 2016). At the continental scale, processes that occurred in the deep past (Fig. 1A), including diversification within lineages during biome expansion with changing paleoclimates (Becerra, 2005; Ackerly, 2009; Edwards et al., 2010; Fine, 2015), may continue to

influence community assembly today (Pennington et al., 2004; Crisp et al., 2009). However, diversification processes can proceed quite differently for different taxa. Well-resolved phylogenies that are dated based on calibrations from the fossil record reveal information about the timing, origins, and pattern of diversification. On the one hand, diversification and expansion of a lineage within a continent through dispersal and allopatric speciation would be expected to cause closely related species to occur in closer proximity and potentially to share more similar climatic niches, while more distantly related species may be expected to occur less frequently and to have more dissimilar climatic niches. In contrast, if diversification occurs through a process of sympatric parallel diversification (Fig. 1B), such that two distinct lineages from a common ancestor have adaptively radiated into contrasting habitats in parallel and in

sympatry, then distant relatives will tend to co-occur locally and may potentially share more similar edaphic and climatic niches than species within a single lineage that are in distal parts of the lineage range (Box 1). Oaks are a prime example of the latter case (Hipp et al., 2018), as are salamanders (Kozak et al., 2009) and damselflies (Stoks and McPeek, 2006) in eastern North America and eucalypts in Australia (Pollock et al., 2015).

In North America, the temperate forest biome became established at high latitudes as the Earth began cooling in the early Paleocene 65–55 Ma (Zachos et al., 2001; Graham, 2011). Continued climate changes (Fig. 1A) led to several periods of minor extinctions, including around 37 Ma (Prothero, 2009) and the contraction of tropical plant taxa to lower latitudes (Crepet and Nixon, 1989; Graham, 2011). The loss of tropical taxa likely created opportunities for expansion and diversification of deciduous eudicots at middle latitudes (Graham, 1999). Dated phylogenetic information from Hipp et al. (2018) reveals that *Quercus* (oaks) radiated in North America starting ca. 35 Ma as the temperate forest biome was expanding southward to middle latitudes (Crepet, 1989; Manos and Stanford, 2001). Four lineages [sections *Protobalanus* (Trelease) Schwarz, *Lobatae* Loudon, *Quercus* L., and *Virentes* Loudon] are inferred to have developed by 30 Ma; the two with high prevalence of deciduousness (*Lobatae* = red oaks; *Quercus* = white oaks) then colonized both western and eastern North America in parallel, diversifying in apparent sympatry nearly simultaneously in eastern North America by 20 Ma, and subsequently radiating southward into Mexico with the increase in volcanism and development of broad elevation gradients in Mesoamerica (Hipp et al., 2018).

We posit that parallel radiation of the oaks into many different habitats along broad climatic gradients in North America (Hipp et al., 2018) is critical to explaining community assembly and phylogenetic structure in forest communities in the continental U.S. (Box 1). Their current abundance, distribution, and local scale co-occurrence patterns may be a consequence of historical contingencies and ongoing environmental sorting or density-dependent ecological processes that reflect early diversification processes. If their history of sympatric parallel diversification has been a critical factor in oak community assembly, effectively allowing twice as many oak species to inhabit a local community as might be expected under allopatric diversification, the highly diverse and abundant oaks (genus *Quercus*) (Nixon, 1997; Cavender-Bares, 2016) in North America may be a consequence of this legacy.

In previous studies of community assembly of the oaks in Florida, we showed that at local scales, (1) both major lineages of oaks occur across the same gradients of soil moisture and fire regime and (2) close relatives co-occur less than expected at random. We proposed that convergence in functional traits and ecological niches could explain these local patterns (Cavender-Bares et al., 2004a, 2004b). At larger spatial extents and when analyses were conducted at broader phylogenetic scales, oaks were clustered in a subset of habitats (Cavender-Bares et al., 2006). Here, we use the U.S. Forest Service (USFS) Forest Inventory and Analysis (FIA) data in plots surveyed across the continental U.S. to examine community assembly at continental scale. The FIA provides abundance data for the majority of the genus with high spatial resolution and continuous coverage across the U.S.; we also harness the highly resolved genome-wide phylogenetic analysis of the American oaks (Hipp et al., 2018). To test the extent to which forces that have operated over vastly different timescales influence community structure at local scales, we examine phylogenetic and trait structure across a suite of shifting grain sizes and with pool

sizes drawn from increasing spatial extents. We examine evolutionary patterns of oak species climatic niches and a suite of functional traits to help illuminate both regional and local assembly processes.

We ask:

1. To what extent do oak species show both diversification and convergence in climatic niches and functional traits as a consequence of parallel adaptive radiation that influences community assembly patterns across North America?
2. To what extent does the oak genus show conservatism in climatic niche, as indicated by occupation of a more constrained climatic space than expected if species were randomly distributed across U.S. forests?
3. Do oak-dominated communities show shifts in community structure with spatial scale consistent with biotic interactions dominating at small spatial scales and environmental sorting at larger scales? Or is phylogenetic community structure relatively invariant with spatial scale, suggesting that the diversification process and resulting pattern dominates patterns of community structure at all scales?
4. How do the biogeographic history of the oaks, including the timing of colonization of different continental regions, and their assembly processes inferred from current community patterns help explain the diversity and abundance of the oaks in North America?
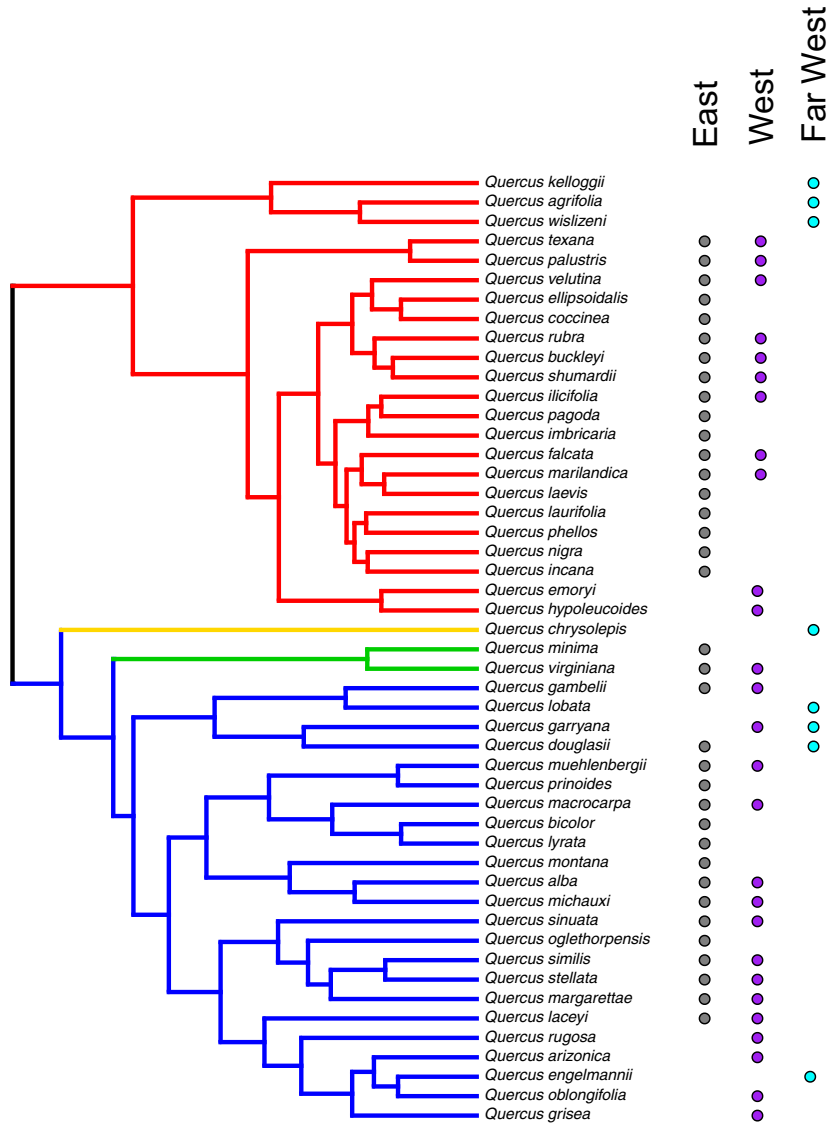
Specifically, we hypothesize that the oaks exhibit convergence in functional traits, corresponding to shared ecological niches among distinct lineages as a consequence of parallel adaptive radiation in sympatry in North America (Box 1: Figs. 1A, 2A). As a consequence, we anticipate that phylogenetic community structure will tend toward overdispersion, while functional trait structure will tend toward clustering across spatial scales (Box 1: Fig. 2G–J). We also expect phylogenetic overdispersion within communities at larger spatial scales than would be expected if local-scale density-dependent and habitat-filtering processes were sufficient to explain community assembly without consideration of the diversification process (Fig. 2G, H in Box 1). In sum, we expect that patterns of community assembly in the oaks across the continental U.S. cannot be explained without consideration of biogeographic history and the diversification process.
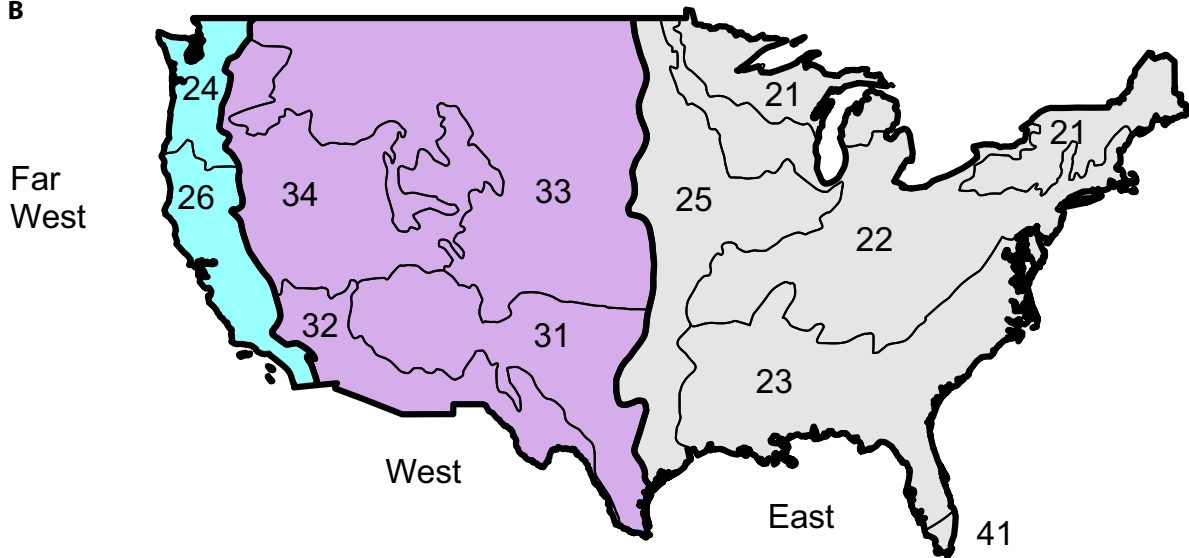
METHODS

Data and data sources

Tree abundance data in U.S. forests—U.S. Forest Service Forest Inventory and Analysis data were obtained from https://apps. fs.usda.gov/fia/datamart/CSV/datamart_csv.html for plots across the U.S., using the fia R package at www.github.com/meireles/fia. The U.S. Forest Service (USFS) surveys stems >2.5 cm dbh in four 7.3-m radius circular "subplots" (168 m²) with a center subplot and three equidistant surrounding subplots, each 36.6 m apart, which together form a "plot" that provides a representative sample of a 6052 m² circular area (44 m radius). The data set was filtered to include only naturally assembled forest plots; dead trees were excluded from the inventory. Only census data from the most recent year available for each plot were accessed. Plots or subplots with no trees were excluded. A fraction of the plots do not follow the

standard design and have more or less than four subplots (https://www.fia.fs.fed.us/library/database-documentation/current/ver70/FIADB%20User%20Guide%20P2_7-0_ntc.final.pdf). Data were filtered for each grain size (see *Data analysis* section below) as follows. At the subplot scale, one subplot was randomly selected from each plot to represent the site for a total of 232,614 subplots (168 m² or similar). At the plot scale, we filtered out all plots that have a design with more than four subplots or with only one subplot containing trees, for a total of 112,183 plots (6052 m² or similar). At larger grain sizes, all plots in the data were used, regardless of design, for a total of 238,460 plots (6052 m² or larger).

Data processing scripts can be found at https://gitlab.com/meireles/compile_fia_data. Diameter of all aboveground stems was used to calculate total basal area of each tree species per subplot. In a small number of cases, trees were only identified to genus. We included *Quercus* spp. for any analyses where presence of the genus was informative but excluded these from any analyses where identity and phylogenetic information was informative. Some discrepancies in taxonomic identification will have slight consequences for total numbers of species but little impact on phylogenetic information (e.g., USFS always identifies *Q. geminata* Small in the southeast as *Q. virginiana* Mill.).

Of the 91 oak species in the continental U.S., only 51 species are in the FIA data set, and only 49 are retained in the analyzed plots (Fig. 2A), which includes only tree species found in naturally assembled forests. Shrub oak species in arid western and southwestern landscapes, for example, are largely excluded from the USFS inventory. Taxonomic names in the FIA data set were matched to the phylogenetic analysis from Hipp et al. (2018). We did not attempt to correct any errors in the identification of oak taxa, even in several cases where individuals were identified well outside their published ranges (Nixon, 1997). These errors are likely few, and there is not a clear way to confirm errors or address them systematically. We used the ecodivision classification and the geographic divisions of the USFS (https://www.fs.fed.us/land/ecosysmgmt) to circumscribe the analyses spatially (see below). Within the lower 48 states, there are three domains, hereafter referred to as geodivisions (East, West, and Far West), and 11 total ecodivisions (Fig. 2B), the names for which we have edited for clarity.

Climate data—High resolution raster data (30 arcsec) from the 19 bioclim climate variables (WorldClim [Hijmans et al., 2005], version 1.4) were associated with the geographic coordinates of plots in the FIA data. The complete set of 238,460 plots (6052 m² or larger) was used. Locations of plots in the FIA database are "fuzzed" to preserve the anonymity and landowners, and occasionally "swapped" between similar plots in the same county. However, the spatial scale of this fuzzing and swapping is likely to be much smaller than the scale of climatic variation. To compare climatic distributions of species within and among clades, we created climate bins using a temperature variable (Bio6) and a precipitation variable (Bio12) based on previous analyses showing that these two variables are useful

orthogonal axes in describing climatic niches of oak species (Pearse and Hipp, 2012; Cavender-Bares et al., 2015). Using the hist function in R, we determined that 20 bins for each climatic variable provided a well-spread distribution for each climatic axis without gaps.

Trait data—We measured (1) specific leaf area (SLA, mm² mg), an important leaf economic spectrum (LES) trait associated with leaf lifespan, resource acquisition, and nutrient use (Wright et al., 2004; Reich, 2014), (2) perimeter per unit leaf area (PLA, cm⁻¹), a leaf trait that increases with degree of lobing and decreases with leaf size and is associated with hydraulic conductance and boundary layer resistance for all species (Sack et al., 2003; Kaproth and Cavender-Bares, 2016), (3) venation length per area (cm⁻¹), associated with leaf hydraulic function (Sack and Scoffoni, 2013), (4) leaf length (mm), (5) petiole length (mm), and (6) stem specific density (g·cm⁻³), associated with mechanical strength and drought tolerance (Cornelissen et al., 2003; Kunstler et al., 2015). Specimens from sunlit branches were pressed and dried alongside samples collected for herbarium specimens as part of the Oaks of the Americas Project (Hipp et al., 2018). Three fully expanded leaves from each individual of each species were scanned and analyzed for leaf surface area, perimeter length, and perimeter per area using ImageJ software (National Institutes of Health, Bethesda, MD, USA); they were then dried and weighed for SLA. Stem specific density was derived from dry segments of stem two to three flushes proximal to the terminal meristem to ensure tissue had lignified. Segments with bark were measured for diameter, length, and mass to calculate cylindrical volume and density. A minimum of three individuals, collected across the species range, were used for each species, with a mean of 16.3 ± 9.7 (SD) individuals per species for each of the FIA 49 species. Forty-seven species had nine or more individual specimens.

Phylogenetic hypothesis—The phylogeny of the American oaks is a highly resolved, genome-wide restriction site-associated DNA sequencing (RAD-seq) phylogeny (Hipp et al., 2018), pruned to match the species in the FIA data set. One species missing from this phylogeny, *Quercus gambelii* Nutt., was added as sister to *Q. lobata* Née based on a recent study by McVay et al. (2017). A phylogeny of the FIA oaks and the geodivisions in which each species occurs is provided in Fig. 2.

Convergence analysis—To capture an integrated measurement of trait space, we chose to assess convergence on the first principal component of the trait matrix PCA ordination (PC1), which accounted for 70% of the variation. We employed two complementary approaches to assess trait convergence between oak lineages. First, we used a reversible-jump Markov chain Monte Carlo simulation (RJMCMC) (Green, 1995) to evaluate convergence scenarios modelled according to an Ornstein–Uhlenbeck process (Hansen, 1997; Butler and King, 2004) as implemented in the program Bayou (Uyeda and Harmon, 2014). This approach estimates the posterior

FIGURE 2. (A) Phylogenetic relationships of the U.S. oaks (*Quercus*) in the FIA database based on Hipp et al. (2018). The four subsections are distinguished by color as follows: red, section *Lobatae*; purple, section *Protobalanus*; green, section *Virentes*; blue, section *Quercus*. The geodivisions where each species occurs are indicated at the tips. (B) Geodivisions (East, West, and Far West) and the 11 ecodivisions within them (21 = northern mixed forest, 22 = eastern broadleaf forest, 23 = southeastern mixed forest, 24 = Pacific lowland mixed forest, 25 = midwestern prairie, 26 = mediterranean, 31 = southwestern subtropical steppe, 32 = southwestern subtropical desert, 33 = temperate steppe, 34 = western temperate desert, 41 = Everglades) from the U.S. Forest Inventory and Analysis (FIA) data and used in establishing null models.

probability that clades experienced shifts in adaptive regime as well as the trait optima associated with those regimes. Bayou's RJMCMC chain was run for 1 million generations and, after checking for convergence, the first 100,000 samples were discarded as burnin. Independent shifts that lead to similar optima were taken as evidence for convergent evolution. Second, we subjected the trait data to an analysis that compared four different models of evolution, (1) a Brownian motion model with a single rate of evolution, (2) an Ornstein–Uhlenbeck (OU) model that assumes a single trait optimum for all oaks, and (3) an OU model that allows for multiple trait optima. When fitting the multiple optima OU models (3), we forced a red oak clade defined by the most recent common ancestor (MRCA) of *Q. velutina* Lam. and *Q. incana* W. Bartram and the white oak clade defined by the MRCA of *Q. muehlenbergii* Engelm. and *Q. alba* L. to converge on the same optimum. These two clades were used on the basis of prior evidence of high similarity of ecological or climatic niches between these two major clades (Cavender-Bares et al., 2004b; Hipp et al., 2018). These models were fit using the mvMORPH package (Clavel, Escarguel, and Merceron, 2015) and selected by comparing their Akaike information criterion (AIC) scores. Finally, we used phenograms (phenogram function in phytools) (Revell, 2012) to visualize trait disparity through time in the two major oak lineages using the Hipp et al. (2018) phylogeny as described above. Given that the phenograms were used for illustration purposes, their internal node values were estimated with maximum likelihood under a Brownian motion model of evolution.

Data analysis

Null models for analysis of species spatial and climatic distributions—A series of null models were used to examine spatial and climatic distributions of the oaks. In the first set, we randomized species relative basal area across all subplots within the three major geodivisions (eastern ecodivisions; western ecodivisions; far western ecodivisions). We repeated the analyses for plots but no qualitative differences were found and are not reported. Randomization within the geographic divisions provides geographic constraints to dispersal and imposes the assumption that over temporal scales relevant to community assembly, dispersal is possible anywhere within the division. We calculated the observed range (2.5 and 97.5% of distribution, to ensure outliers were not included) of oak tree species across 19 climatic axes (all 19 bioclim variables), and the observed occupancy of forest subplots by oaks, compared to null expectations when the basal area of all oak tree species is randomized across all U.S. forest subplots. The comparison of the observed 95% climatic range of oaks compared to the null model allows interpretation of whether oak tree species have a smaller climatic envelope than that occupied by all forest tree species in the continental U.S. It thus tests for greater clustering or greater climatic breadth of the oak genus in climatic space than expected at random. Oak occupancy, or proportion of total natural forest area inhabited by oaks, was calculated as the total number of subplots with at least one oak species × subplot area/total surveyed forested area. Comparing the observed oak occupancy to the null model detects whether oak tree species cluster geographically within the geodivisions more than expected given the extent of U.S. forests.

A second set of analyses was conducted to test whether oaks are more clustered than expected among subplots or plots within their observed climatic envelope. Here we excluded all plots that occur within climatic bins not inhabited by at least one oak species (which

removed 2766 subplots from the subplot-level analysis and 603 plots from the plot-level analysis). Again, we randomized species relative basal area across all plots within the three major geodivisions. Here and in all subsequent analyses at the subplot scale, one subplot per plot was randomly selected to avoid spatial autocorrelation that would result from using multiple subplots per plot at the same site. Within the climatic envelope inhabited by oaks, we calculated (1) the proportion of total forest area occupied by oaks as the total number of subplots or plots with at least one oak species × plot area/total forested plot area; (2) the proportion of total forest area with at least one oak species that has more than one oak; (3) the average number of oak species per subplot and plot with at least one oak, which indicates whether oak species tend to co-occur more frequently than expected; and (4) the average number of co-occurring oaks from different oak sections (*Lobatae*, *Quercus*, *Virentes*, *Protobalanus*) in subplots and plots with at least one oak. The latter indicates whether species of different *Quercus* sections tend to co-occur more than expected by chance, which may indicate complementary interactions among species of different lineages. Greater co-occurrence than expected of different lineages is a coarse measure of phylogenetic or taxonomic overdispersion within the oak clade.

Analyses of phylogenetic and trait structure at multiple spatial extents and grain sizes—In the third set of analyses, we addressed the extent to which phylogenetic structure and trait structure (for two leaf traits, SLA and PLA, associated with resource use and stress tolerance) of oak communities change with spatial extents and grain sizes. These analyses were designed to test the hypotheses posited in Fig. 2G–J in Box 1. For these analyses, we excluded all subplots, plots, or cells (depending on grain size) that did not contain at least two oak species, retaining 110,225 of 398,987 subplots, from which one subplot per plot was randomly selected, and 30,048 of 54,050 plots. Null models were run to examine both the phylogenetic structure of communities and trait structure of communities using a tip-swap algorithm in which species were randomized across the phylogeny, holding the topology of the phylogeny constant. To calculate trait distances, we scaled each value for each trait from 0 to 1 and calculated Euclidean distances between species.

In a first set of analyses, the goal was to test the consequences of increasing the spatial extent (Box 1: Fig. 2H, J) from which the pool size is generated. For these, the grain size was set at 168 m², but the spatial extent from which the pool was drawn increased from 287.9 km² to entire geodivisions. The oak phylogeny was pruned to the oak species pool within each spatial extent for each observed and null model calculation of trait and phylogenetic structure. In a second set of analyses, the goal was to test the consequences of increasing the grain size (Box 1: Fig. 2G, I). Observed and null model calculations were repeated sequentially at nine grain sizes, the first two of which included the 168 m² FIA plots nested within their larger ~6052 m² plots, and then by aggregating the FIA plots into larger hexagonal cell sizes ranging from 10.7 to 7774.2 km²) (Appendix S1). Aggregation of plots was accomplished using the dggridR package in R (Barnes, 2016), which uses a nearly even grid of hexagons to avoid spatial distortions that lead to uneven cell sizes with changes in latitude. The oak phylogeny was pruned either to the oak species pool within each geodivision or to the ecodivisions within each geodivision. To limit the complexity of the analyses, we chose not to increase both grain size and spatial extent of the pool together. We calculated four metrics of phylogenetic community structure and trait community structure. For phylogenetics, we used
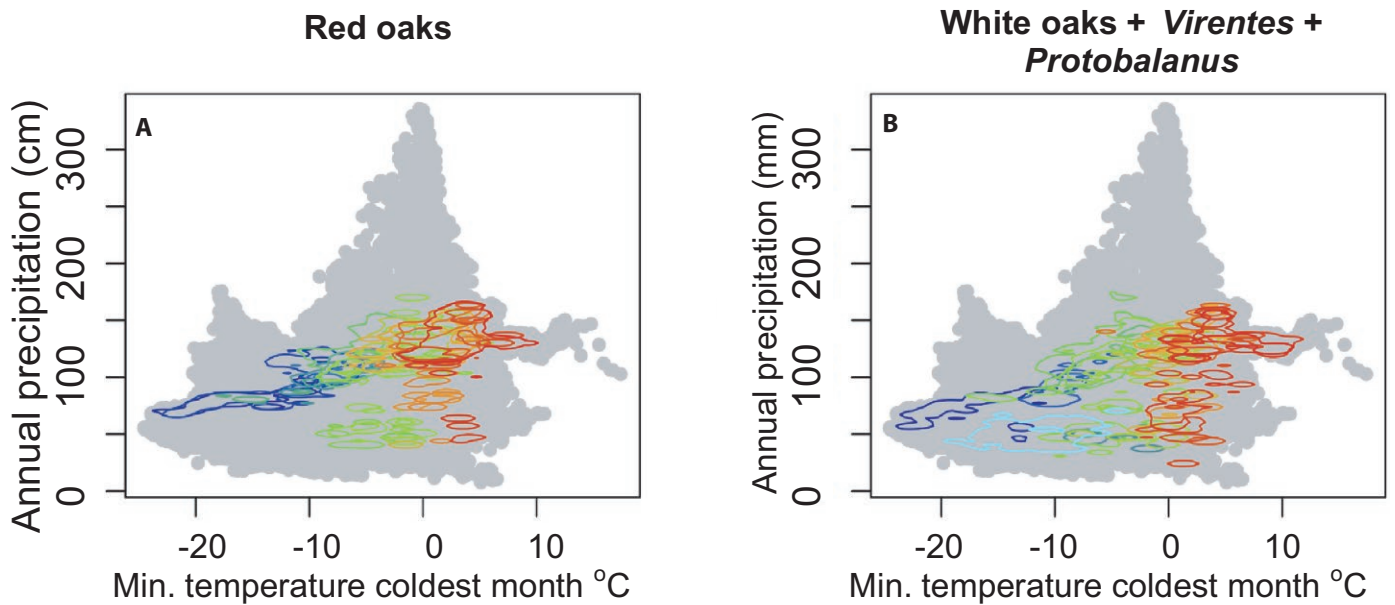
Red oaks

White oaks + *Virentes + Protobalanus*

FIGURE 3. The two major American oak lineages show very similar climatic distributions. (A) Density plot of the climatic distribution of all species in the red oak lineage, *Quercus* section *Lobatae*, superimposed over the climatic distribution of all forest plots in the continental U.S. along two axes, mean minimum temperature in the coldest month and mean annual precipitation. (B) Density plot of the lineage that includes *Q.* sections *Quercus*, *Virentes*, and *Protobalanus*. Within the U.S. forest climatic envelope defined by the distribution of U.S. FIA plots along two climatic axes—minimum temperature in the coldest month (range: −28°C to 19°C) and mean annual precipitation (range: 1 to 398 cm per year)—each oak lineage spans nearly the full minimum temperature range and about two thirds of the annual precipitation range; filled gray circles represent all U.S. FIA plots. Colored contours show climatic distributions of individual oak species.

mean phylogenetic distance (MPD; a measure of the mean phylogenetic branch length distances between species); mean nearest taxon distance (MNTD; a measure of the phylogenetic distances between closest relatives in a community) using presence/absence data; and MPD and MNTD using abundance weighted values (Webb, 2000; Webb and Donoghue, 2005) for the observed data, and we compared those values to values generated from the null models to obtain standardized effect sizes (SES) of overdispersion or clustering using Picante (Kembel et al., 2010). For community trait structure, mean trait distance (MTD) and mean nearest taxon trait distance (MNTTD) metrics were calculated exactly the same way but using the trait distance matrix rather than the phylogenetic distance matrix. Analyses were limited to plots with at least two oak species.

We also tested whether co-occurrence was associated with phylogenetic distance (Cavender-Bares and Wilczek, 2003; Cavender-Bares et al., 2004b) using quantile regression (Slingsby and Verboom, 2006). Within the three major geographic divisions, we compared observed quantile regression slopes to those generated from null models in which relative basal area of species was randomized across subplots within each geodivision or in which species were randomized across the phylogeny, holding the topology of the phylogeny constant.

Results

Climatic and spatial distributions of U.S. oak species—The two large clades (red oaks and white oaks+*Virentes*+*Protobalanus*) have very similar climatic distributions (Fig. 3). Within the U.S. forest climatic envelope defined by two climatic axes, minimum temperature in the coldest month (range: −28°C to 19°C) and mean annual

precipitation (range: 1 to 398 cm·yr⁻¹), each spans nearly the full minimum temperature range and a substantial fraction of the annual precipitation range. Most oak species distributions fall within −10°C and 10°C and between a mean of 50 and 160 cm precipitation per year. Null model simulations confirm that in the eastern and far western geographic divisions, oak tree species occupy a significantly narrower climatic envelope than all U.S. forest trees, indicating that they did not radiate into all possible climatic niches available in forested biomes (Table 1). At the subplot scale, this pattern holds in the eastern geographic division for nearly all climatic variables (16 of 19 variables), except for mean temperature of wettest quarter (Bio8), precipitation of driest month (Bio14), and precipitation of driest quarter (Bio17), for which oak tree species actually inhabit a greater climatic range than expected. In other words, in the east, oaks occupy a broader precipitation gradient than expected but are excluded from very cold environments. In the far western geographic division, oaks also occur within a narrower climatic range than expected for nearly all variables (17 of 19 variables), except for isothermality [(mean diurnal temperature range)/mean annual temperature range)] (Bio3) and temperature seasonality (Bio4). Oaks are thus excluded from forested areas with very low temperatures and very high precipitation levels but occur across the full range of isothermality and temperature seasonality. In the western geographic division, however, oaks occur in a narrower climatic range than expected for some variables, including annual mean temperature (Bio1), maximum mean temperature of the warmest month (Bio5), mean temperature of the wettest quarter (Bio8), mean temperature of the warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), annual precipitation (Bio12) and precipitation of the wettest month (Bio13), but inhabit a broader climatic

TABLE 1. The observed range (2.5 and 97.5% of distribution) of oak tree species across 19 climatic axes, and the observed occupancy of forest subplots by oaks, compared to null expectations when the basal area of all oak tree species is randomized across all U.S. forest subplots. BIO1 = annual mean temperature, BIO2 = mean diurnal range [mean of monthly (max temp − min temp)] (°C), BIO3 = isothermality (BIO2/BIO7) (× 100), BIO4 = temperature seasonality (standard deviation × 100), BIO5 = max temperature of warmest month (°C), BIO6 = min temperature of coldest month (°C), BIO7 = temperature annual range (BIO5-BIO6) (°C), BIO8 = mean temperature of wettest quarter (°C), BIO9 = mean temperature of driest quarter (°C), BIO10 = mean temperature of warmest quarter (°C), BIO11 = mean temperature of coldest quarter (°C), BIO12 = annual precipitation (mm), BIO13 = precipitation of wettest month (mm), BIO14 = precipitation of driest month (mm), BIO15 =precipitation seasonality (coefficient of variation), BIO16 = precipitation of wettest quarter (mm), BIO17 = precipitation of driest quarter (mm), BIO18 = precipitation of warmest quarter (mm), BIO19 = precipitation of coldest quarter (mm).

Climate Variable	East					West					Far West				
	Obs range		Null range		P	Obs range		Null range		P	Obs range		Null range		P
BIO1	4.8	**20**	3	20	0.001	3.6	19.5	−1	19	0.001	8.2	16.2	4	15	0.001
BIO2	**10.8**	**14.1**	10	14	0.001	*12.6*	*19.7*	*12*	*19*	1*	11.6	17.2	9	17	0.001
BIO3	**26**	**45**	25	45	0.001	*29*	*52*	*31*	*50*	1*	42	61	37	57	0.118
BIO4	5793	**11,675**	5862	12,293	0.001	*6058*	*11,451*	*6374*	*10,307*	1*	3182	6899	3053	6896	0.058
BIO5	**25.7**	**34.3**	24	34	0.001	23.5	35.6	19	36	0.001	24	35.9	20	35	0.001
BIO6	**−19**	**4.8**	−23	5	0.001	*−18.1*	*2.8*	*−19*	*1*	0.986*	−5.3	**4**	−9	3	0.001
BIO7	**280**	**466**	280	488	0.001	*303*	*470*	*322*	*452*	1*	204	356	183	364	0.001
BIO8	*4.5*	*26.8*	5	27	0.992*	−2.5	24.3	−9	25	0.001	1.2	10.8	−2	9	0.001
BIO9	**−10.9**	**26.1**	−14	24	0.001	*−8.9*	*18.2*	*−9*	*18*	1*	15.3	25.1	12	24	0.001
BIO10	**18**	**27.2**	16	27	0.001	14.1	28	9	28	0.001	15.6	25.1	12	24	0.001
BIO11	**−11**	**12.2**	−14	12	0.001	−9	10.4	−11	9	0.001	0.9	10.3	−3	9	0.001
BIO12	736	**1579**	658	1563	0.001	366	814	256	866	0.001	403	1730	416	2681	0.001
BIO13	94	**187**	91	186	0.001	46	125	31	120	0.001	72	314	61	444	0.001
BIO14	*18*	*101*	14	95	1*	7	40	8	41	0.411	0	13	1	47	0.001
BIO15	**9**	**52**	10	57	0.001	*16*	*78*	*11*	*71*	1*	62	91	41	89	0.001
BIO16	264	**515**	253	515	0.001	125	310	84	330	0.001	203	873	169	1268	0.001
BIO17	65	*329*	55	318	1*	30	139	29	142	0.001	3	70	8	187	0.001
BIO18	238	**500**	233	505	0.001	94	273	63	248	0.026	7	83	11	206	0.001
BIO19	65	**436**	55	429	0.001	35	197	32	304	0.001	196	854	157	1188	0.001

Occupancy	Proportion of forest subplots			Proportion of forest subplots			Proportion of forest subplots		
	Obs	Null	P	Obs	Null	P	Obs	Null	P
	0.368	0.397	0.001	0.090	0.095	0.001	0.229	0.231	0.044

Bold: narrower climatic range or occupancy than expected at random.
*Broader distribution on climatic axis than expected at random.

range than expected for a number of others, including mean diurnal range (Bio2), isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of the coldest month (Bio6), temperature annual range (Bio7), mean temperature of the driest quarter (Bio9), and precipitation seasonality (Bio15). In other words, they occupy a wide range of seasonalities but are again excluded from very cold environments and those with very high precipitation.

At the subplot scale, the proportion of oak tree communities that have at least two different oak species is significantly greater than expected in eastern and western geodivision and in most ecodivisions (Table 2A). The exception is the mediterranean ecodivision within the Far West, which shows fewer species per oak community than expected. Likewise, the eastern and western geodivisions have a greater number of oak species per subplot than expected within the oak climatic envelope, with the exception of the far western eco-division and the mediterranean ecodivision, which had fewer oak species per subplot within the oak climatic envelope. The eastern and western geodivisions also have a greater number of oak clades (sections of the genus) within a subplot than expected. The same holds true for most of the ecodivisions, except the mediterranean, which has fewer sections per subplot than expected.

At the plot scale, all three geodivisions have a greater number of oak species per oak community than expected, a greater number of oak species than expected per oak community within their climatic envelope, and a greater number of oak clades per community than

expected by chance (Table 2B). None of the ecodivisions show a contrary pattern, although some are not significant for these patterns. Thus, at the plot scale, multiple oak species, and multiple oak clades, consistently co-occur more than expected by chance.

Species and lineage distribution and diversity patterns—Within the continental U.S., more oak species occur in the eastern geographic division (36) than in the western (29) or far western (8) (Fig. 2). Oaks show highest numbers of species in the southeastern United States (33 of the 36 species in the eastern geodivision), particularly in ecosubregions that have considerable topographic variation (Fig. 4A). Relatively fewer oak tree species occur in coldest climates (12 in the northern mixed forest ecodivision), and very few occur in the Pacific lowland mixed forest ecodivision (3) or the western temperate desert ecodivision (2) (Fig. 4A), although the latter pattern reflects the fact that shrub oaks are not counted.

Within the genus, red oaks (*Quercus* section *Lobatae*) and white oaks (*Quercus* section *Quercus*) cover a large fraction of the eastern geodivision and the mediterranean ecodivision of the far western geodivision, but they are sparser through the western geodivision (Fig. 5B, C). The two sections have largely overlapping spatial distributions, with the exception that a single white oak species (*Q. gambellii*) occurs in the upper montane west (Fig. 5A). In the eastern geographic division, there are 18 red oak species, 16 white oak species and two live oak species. In the western division, there are

TABLE 2. The observed average values relative to null expectations for (1) the proportion of subplots (A) or plots (B) where two or more oak species occur from all subplots (or plots) that have at least one oak, (2) the average number of oaks that occur within subplots or plots from those with at least one oak species, and (3) the number of oak clades (sections of the genus) that occur within subplots or plots with at least one oak species within each of the three U.S. geodivisions and 11 ecodivisions within those where oaks occur. The null models for 1 and 2 randomized the basal area of each oak species across all subplots or plots within the oak climatic envelope; the null model for three randomized the basal area of each oak species across all subplots or plots with at least one oak. In A, the subplots were 168 m². One subplot that met the criteria of having an oak was randomly selected within a ~6052 m² plot. In B, the plots were ~6052 m².

	Do oaks co-occur more often than expected?			Do more oak species co-occur than expected?			Do more oak clades co-occur than expected at random?		
	Proportion of oak subplots with two or more oak species			Number of oaks per subplot			Number of oak sections per subplot		
	Oak spp. abundance values randomized within the oak climatic envelope						Oak spp. abundance randomized across oak subplots		
	Obs	Null	≤ Simulated	Obs	Null	≤ Simulated	Obs	Null	≤ Simulated
A. Geodivisions									
East	0.31	0.22	1***	1.38	1.25	1***	1.23	1.13	1***
West	0.09	0.04	1***	1.09	1.04	1***	1.08	1.02	1***
Far West	<u>0.10</u>	0.13	0.017*	<u>1.11</u>	1.13	0.015*	1.09	1.10	0.298
Ecodivisions									
Northern mixed forest (21)	0.15	0.05	1***	1.17	1.05	1***	1.13	1.03	1***
Eastern broadleaf forest (22)	0.37	0.31	1***	1.48	1.37	1***	1.30	1.20	1***
Southeastern mixed forest (23)	0.29	0.26	1***	1.35	1.31	1***	1.19	1.15	1***
Pacific lowland mixed forest (24)	0.01	0.00	0.88*	1.01	1.00	0.88**	1.01	1.00	1***
Midwestern prairie (25)	0.22	0.21	0.949ms	1.26	1.24	0.953ms	1.18	1.14	1***
Mediterranean (26)	<u>0.11</u>	0.19	0.001***	<u>1.12</u>	1.22	0.001***	<u>1.10</u>	1.16	0.001***
Southwest subtropical steppe (31)	0.10	0.09	0.988***	1.10	1.09	0.987***	1.09	1.06	1***
Southwestern subtropical desert (32)	0.32	0.08	1***	1.35	1.08	1***	1.31	1.05	1***
Temperate steppe (33)	0.00	0.01	0.041ms	1.00	1.01	0.041ms	1.00	1.00	0.994***
Western temperate desert (34)	0.00	0.00	0.646	1.00	1.00	0.646	1.00	1.00	-
Everglades (41)	0.22	0.04	0.999***	1.22	1.04	0.999***	1.22	1.04	1***

	Proportion of oak plots with two or more oak species			Number of oaks per oak plot			Number of oak sections per oak plot		
	Oak spp. abundance values randomized within the oak climatic envelope						Oak spp. abundance randomized across oak plots		
	Obs	Null	≤ Simulated	Obs	Null	≤ Simulated	Obs	Null	≤ Simulated
B. Geodivisions									
East	0.61	0.46	1***	2.05	1.63	1***	1.50	1.30	1***
West	0.16	0.07	1***	1.19	1.07	1***	1.13	1.04	1***
Far West	0.32	0.20	1***	1.36	1.22	1***	1.31	1.16	1***
Ecodivisions									
Northern mixed forest (21)	0.29	0.11	1***	1.37	1.11	1***	1.25	1.07	1***
Eastern broadleaf forest (22)	0.68	0.60	1***	2.22	1.92	1***	1.60	1.43	1***
Southeastern mixed forest (23)	0.65	0.59	1***	2.15	1.92	1***	1.48	1.40	1***
Pacific lowland mixed forest (24)	0.03	0.01	0.986**	1.03	1.01	0.986**	1.03	1.01	0.986**
Midwestern prairie (25)	0.54	0.42	1***	1.79	1.57	1***	1.47	1.30	1***
Mediterranean (26)	0.36	0.34	0.897	1.41	1.41	0.493	1.34	1.28	1***
Southwest subtropical steppe (31)	0.19	0.15	1***	1.21	1.16	1***	1.14	1.09	1***
Southwestern subtropical desert (32)	0.54	0.14	1***	1.67	1.15	1***	1.52	1.10	1***
Temperate steppe (33)	0.01	0.01	0.373	1.01	1.01	0.373	1.01	1.00	1***
Western temperate desert (34)	0.00	0.00	0.552	1.00	1.00	0.552	1.00	1.00	-
Everglades (41)	0.35	0.11	1***	1.35	1.11	1***	1.32	1.11	1***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P = 0.001$
Underlined values indicate observed are lower than expected; otherwise, significance indicates observed values are greater than expected.

slightly more white oak species (15) than red oak species (13), and one live oak. In the far west, there are similar numbers of red oaks (3) and white oaks (4), as well as one species of golden cup oaks in the FIA data. Consistent with prior observations, *Virentes* are restricted to warm climates with high annual precipitation (Cavender-Bares et al., 2015), and *Protobalanus* occurs only in dry mediterranean regions (Manos et al., 1999). In all three geographic divisions, oaks occur in fewer forest plots than expected (Table 1), indicating that oak tree species (at least those >1 cm dbh) are excluded from some forested habitats within their climatic envelope.

Niche and trait convergence—We identified four evolutionary regime shifts with posterior probabilities greater than 0.3 (Fig. 4A). A white oak clade [defined here as the least inclusive clade that contains *Q. muehlenbergii* and *Q. margarettae* (Ashe) Small], which corresponds to eastern white oaks, and a red oak clade
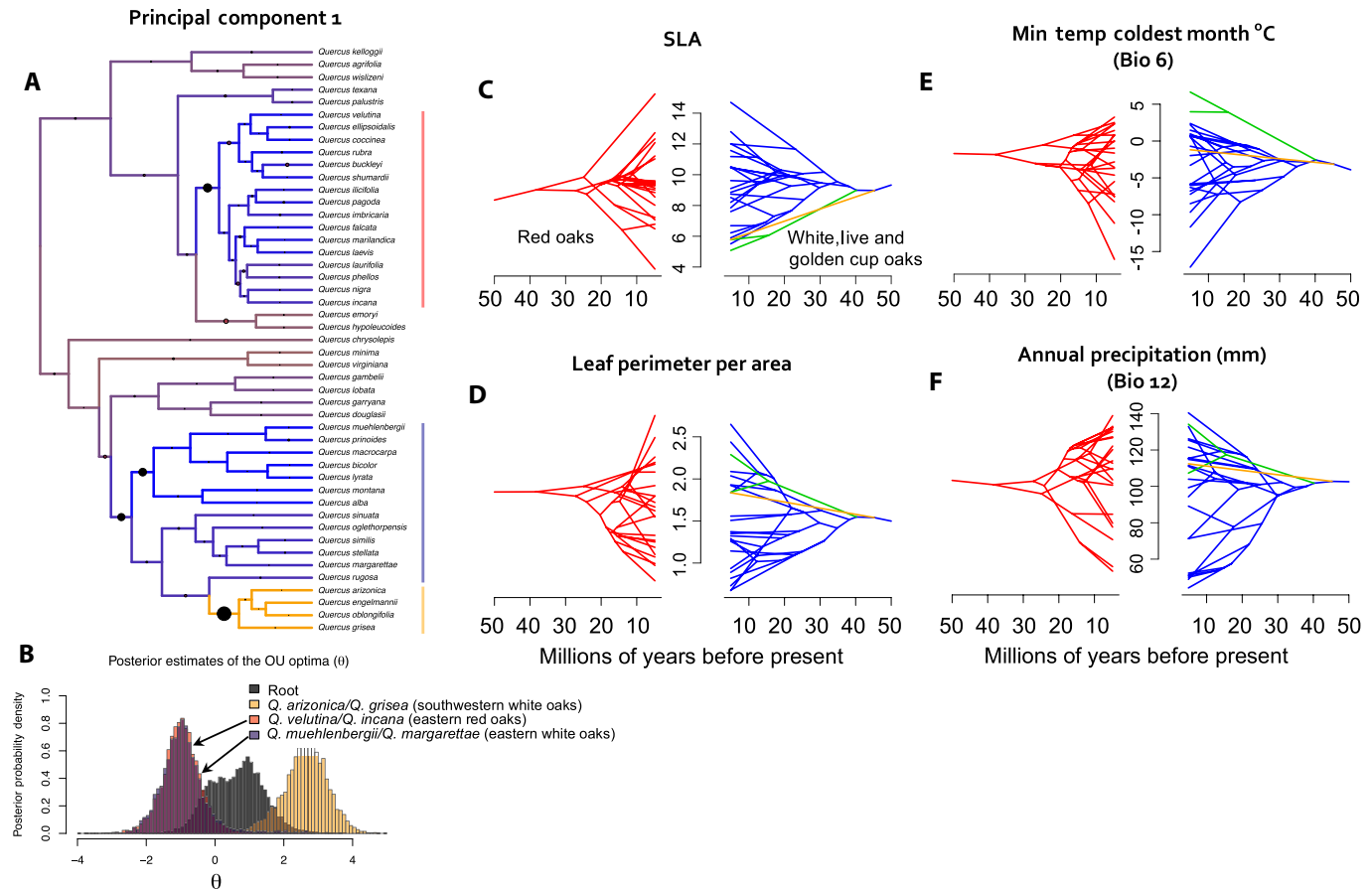
FIGURE 4. Convergence in plant function between the major oak lineages. (A) Branch colors indicate different optima inferred from an OU model for the first principal component of a multivariate trait matrix that includes perimeter per unit area (cm⁻¹), specific leaf area (mm²·mg), venation length per area (cm⁻¹), leaf length (mm), petiole length (mm), and stem specific density (g·cm⁻³). Circles indicate evolutionary shifts and circle size are proportional to posterior probability that a shift occurred on the branch indicated; black circles indicate shifts with posterior probability greater than 0.3. The vertical bars to the right indicate regions of each major clade that have experienced a regime shift. Histograms depict the posterior density of trait optima (θ) associated with three of the four regime shifts estimated from the Ornstein–Uhlenbeck (OU) model. The histogram colors match the vertical bars on the phylogeny, defining the species group associated with each regime shift. Part of the red oaks (in red) and white oaks (blue) largely overlap in their inferred trait optima, supporting the hypothesis of convergence between the two groups. Phylogenetic traitgrams for the two major lineages are shown for specific leaf area (B) and leaf perimeter per unit area (C). Species mean climatic values across their ranges are also shown for two climatic axes: mean minimum temperature of the coldest month (°C) (D) and mean annual precipitation (cm) (E). In B–E, the red oak clade is shown on the left (red color) and the clade containing the white oaks (blue), eastern live oaks (green), and the golden cup oak (gold) is shown on the right of the trait or climate axis.

(the least inclusive clade that contains *Q. velutina* and *Q. incana*), which corresponds to eastern red oaks, are associated with evolutionary shifts that share similar trait optima (Fig. 4A), suggesting that these lineages converged to the same trait space. We further examined the convergence between the eastern red and white oak clades by comparing the fit of different trait evolution models. A two-optima OU model that forces a red oak clade and a white oak clade (Fig. 4A, vertical bars on the right) to be convergent is preferable (AIC 316.4739) to models that do not imply convergence, specifically, a single rate Brownian motion model (AIC 327.0075) and a single optima OU model (AIC 324.8428). Overlapping optima for multivariate plant function for the eastern red and eastern white oak clades (Fig. 4B) provide evidence for ecological convergence supporting the hypothesis of sympatric parallel adaptive radiation.

Ecological convergence is further supported by patterns of diversification of individual functional traits and species climatic niches (Fig. 4C, D), consistent with prior studies at regional scales (Cavender-Bares and Holbrook, 2001; Cavender-Bares et al., 2004a, 2004b) and at the continental scale (Hipp et al., 2018). The two major clades (the red oaks and an inclusive white oak clade that includes the *Virentes* and *Protobalanus*) examined side by side show that diversification of the climatic niches and functional traits occurred at similar rates and over similar time periods from 30 to 10 Ma (no significant divergence from the expectation of homogeneous disparity through time was detected).

Phylogenetic and trait community structure: geographic variation and shifts across spatial scales—Phylogenetic dispersion patterns in the U.S. oaks, averaged by geodivision, were consistently
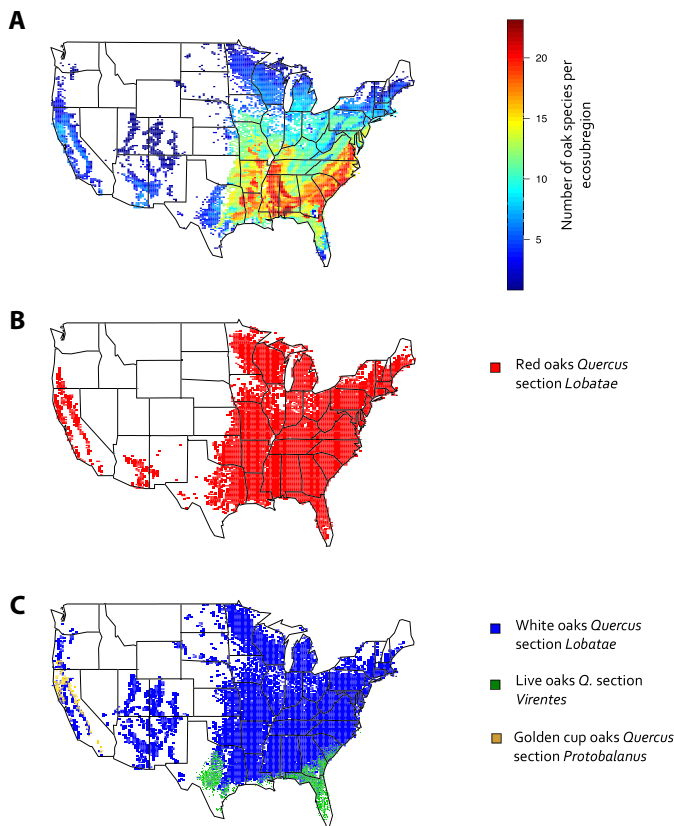
FIGURE 5. (A) Oak species diversity patterns across the continental U.S. based on U.S. Forest Service data showing, for each ecosubregion, a color value indicating the number of oaks species in the whole ecosubregion. Ecosubregions are classifications of forest ecosystem types nested within the ecodivisions demarcated in Fig. 2. (B) Distribution of *Quercus* section *Lobatae* (red oaks). Colors indicate species richness levels. (C) Distribution of *Quercus* section *Quercus* (white oaks), section *Virentes* (eastern live oaks), and section *Protobalanus* (golden cup oaks).

overdispersed at small grain sizes regardless of spatial extent in the eastern, western, and far western geodivisions (Fig. 6C–E). In contrast, trait dispersion tended to be clustered across the U.S. (Fig. 6A, L, M), particularly at large spatial extents (Fig. 6F) and at large grain sizes (Fig. 6L), except in the far western geodivision where traits were overdispersed at all spatial extents and grain sizes (Fig. 6H, N). Dispersion patterns varied geographically (Fig. 6A, B). Phylogenetic overdispersion was most pronounced at higher latitudes, as well as throughout the Midwest and in Florida, but communities were not different from random expectation or were clustered in the highly diverse middle latitude belt in the southeast where oak diversity is high (Fig. 6A). Greatest trait clustering was also in the middle latitude belt but extended throughout the western and southern United States including Florida (Fig. 6B). Like phylogenetic structure, patterns of trait structure were fairly consistent with spatial extent, but showed greater clustering at larger grain sizes or a shift from overdispersion toward clustering in the east, as anticipated (Box 1: Fig. 2G, I).

Results for presence/absence and abundance-weighted metrics as well as mean distances and nearest taxon distance were highly similar at small grain sizes across spatial extents (Fig. 6C–H). However, different metrics showed somewhat different patterns in the highly diverse eastern geodivision. Here, phylogenetic clustering was most pronounced when examined among closest relatives (MNTD), without abundance weighting, such that rare species have higher impact. The pronounced clustering using the MNTD metric likely reflects the increasing richness within each major clade as grain size is increased: inevitably, the distance between closest relatives narrows as more species are added. In contrast, mean phylogenetic distances between species, taking abundance into account, remained overdispersed or the same as random expectation (which is equal abundance of species from two major clades). In far western Californian and Oregonian oak forests, communities are phylogenetically and functionally overdispersed at all grain sizes, regardless of metric (Fig. 6E, H, K, N).

Phylogenetic and trait dispersion patterns calculated using quantile regression (Appendix S1; see the Supplemental Data with this article) were also largely consistent with results using the Webb metrics. In the eastern geodivision, there was a general shift from phylogenetic overdispersion to clustering, while traits were clustered and showed a strong increase in trait clustering with increasing grain size. In the western geodivision, there was significant phylogenetic overdispersion at many grain sizes and a general pattern of trait clustering that increased with grain size. In the far western geodivision there was consistent phylogenetic overdispersion across scales, but trait patterns were not different from random. Both kinds of analyses show the same general pattern of significant phylogenetic overdispersion accompanied by trait clustering.

DISCUSSION

We find in oak-dominated forest communities across the United States, in assemblages of small size, that oaks are phylogenetically overdispersed, while leaf functional traits linked to environmental sorting are more similar than expected, except in the far western geodivision, where leaf traits are also overdispersed. The oaks, as a group, have expanded to fill a broad climatic range, although they are excluded from the coldest and wettest forest regions in the United States (Table 1). Geographic and climatic distributions of the major clades are largely overlapping (Figs. 3, 5), and functional traits show convergence between major clades within the white and red oak lineages (Fig. 4A, B), such that the ranges of trait values and climatic distributions show parallel coverage within the major oak clades (Fig. 4C–F). We argue that the highly repeated community patterns of phylogenetic overdispersion at local scales are a consequence of sympatric parallel diversification in the oaks (Hipp et al., 2018) that initiated at the continental scale over 35 Ma with the expansion of the temperate zone. The diversification process accounts for the highly similar geographic distributions, climatic niches, and convergence in functional traits within the two broadly distributed oak clades. These continental patterns mirror local-scale patterns in northern central Florida showing parallel ecological and functional trait diversification into hydrologic niches in *Lobatae* (red) and *Quercus* (white) oaks, accounting for greater co-occurrence of distant relatives than expected at random (Cavender-Bares et al., 2004a, 2004b, 2006). The strongest patterns of overdispersion occur at the smallest grain sizes, suggesting that interspecific interactions are likely important in community assembly and may have been important in the divergence of species into contrasting habitats. Complementarity mechanisms may promote the co-occurrence of phenotypically similar oaks from different lineages, a phenomenon that may have been critical throughout the diversification process.
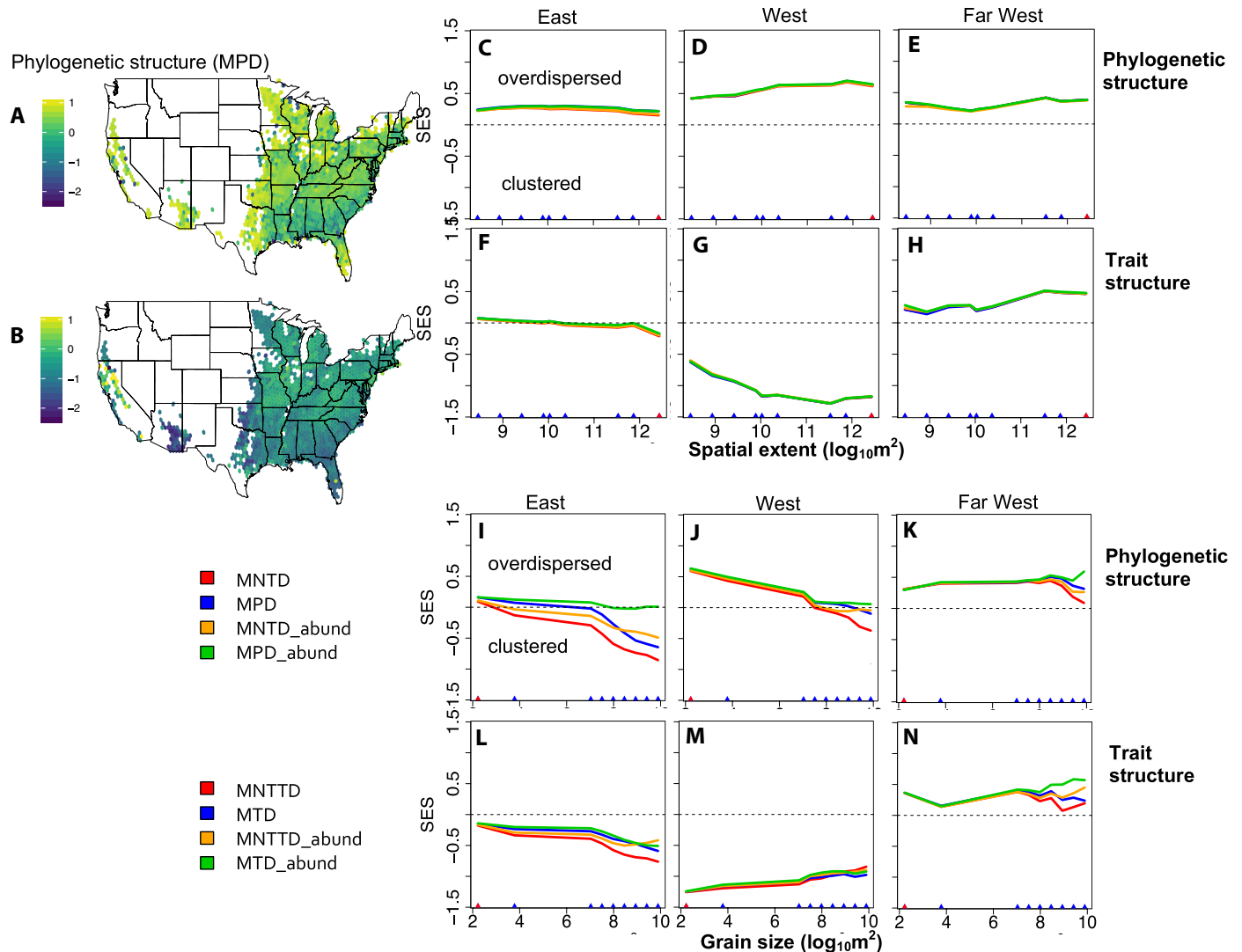
FIGURE 6. Maps of (A) the phylogenetic and (B) trait dispersion ("structure") of oak communities (calculated as the standardized effect size (SES) of the mean phylogenetic distance (MPD), not abundance weighted) at the smallest grain size (258 m²) and aggregated to the ~2600 km² scale (size of hexagons) across the U.S. Average phylogenetic and trait dispersion of oak communities in East, West, and Far West geodivisions when community grain size is held constant at the smallest size (168 m²), but the spatial extent from which the oak species pool is drawn is increased from 287.9 km² to entire geodivisions (C–H) and when community grain size is increased from 168 m² to 7774.2 km² (I–N). Phylogenetic structure is calculated as the SES for four dispersion metrics (mean phylogenetic distance [MPD], mean nearest taxon distance [MNTD], MPD-abundance weighted, MNTD-abundance weighted), and trait structure is calculated for parallel metrics using trait distance matrices rather than phylogenetic distance matrix (mean trait distance [MTD], mean nearest taxon trait distance [MNTTD], MTD-abundance weighted, MNTTD-abundance weighted). Legends for these metrics are the same for spatial extent (upper panels) and grain size (lower panels). Small triangles on the x-axes indicate the spatial extents (C–H) and grain sizes (I–N) of the analyses. The red triangles in C–H and I–N correspond to the same grain size and spatial extent.

The community patterns we find in North American oaks bear a striking resemblance to the repeated body size patterns in coexisting clades of North American salamanders (Kozak et al., 2009). Distinct clades of salamanders have radiated in body size and coexist in the same microhabitats, sharing more similar body sizes than expected at random. In salamanders, these patterns appear to contradict the hypothesis of preemptive evolution, whereby radiation of one lineage is expected to preempt the radiation of subsequent lineages in the same geographic region as ecological space becomes filled (Losos et al., 1998; Schluter, 2000). In the case of the oaks, we hypothesize that sympatric parallel diversification has driven community assembly

patterns over evolutionary timescales as follows: early on, ecological space became available as the temperate biome emerged and tropical taxa waned (Crepet, 1989; Graham, 2011) allowing expansion of lineages, like the oaks, adapted to seasonal temperate climatic conditions. The range retraction of tree species that previously occurred in North America provided opportunity for diversification of the oaks into novel adaptive zones (Cavender-Bares et al., 2016), following classic theory of adaptive radiation (Simpson, 1953; Schluter, 1996; Givnish et al., 2009). During diversification, ecological interactions among oak populations drove phenotypic and habitat divergence. Co-occurrence of close relatives was likely prevented by shared

disease susceptibility that would have increased density-dependent mortality, and incomplete reproductive isolation that would have precluded the persistence of closely related species in close spatial proximity (Levin, 2006; Larcombe et al., 2015; Pollock et al., 2015). Once divergent phenotypes were established, co-occurrence would have been prevented by trait–environment sorting since close relatives would have fitness advantages in contrasting habitats. At the same time, coexistence of tree species from distinct lineages incapable of gene flow but adapted to the same ecological habitats were likely promoted by complementarity mechanisms, including reduction of density-dependent mortality linked to enemies.

Phylogenetic overdispersion has been found in *Anolis* lizards (Losos et al., 2003), mammalian predators (Davies et al., 2007), and bacterial assemblages (Horner-Devine and Bohannan, 2006), among other systems, and is often interpreted as evidence for competitive exclusion. However, it can also result from other processes (Gerhold et al., 2015), such as environmental sorting processes linked to traits that are convergent (Cavender-Bares et al., 2004b). The possibility that sympatric parallel diversification would be expected to cause overdispersion is not well appreciated, particularly in the plant literature. Long after the most dynamic phases of diversification, the functional patterns of species established by their evolutionary history likely continue to drive community assembly.

Divergence of close relatives and mechanisms of complementarity among distant relatives—Adaptive radiation requires mechanisms that allow splitting and isolation of populations, including adaptive shifts to contrasting habitats or allopatric speciation events involving mechanisms of vicariance. The functional divergence of close relatives is a signature of ecological niche shifts associated with adaptive radiation (Schluter, 2000; Gillespie, 2004; Kozak et al., 2005; Givnish et al., 2009; Keller et al., 2013; Hernández-Hernández et al., 2014). Gene flow prevents close relatives with incomplete reproductive isolation from co-occurring over multiple generations in the absence of habitat separation (Gailing and Curtu, 2014; Pollock et al., 2015). Enemy pressure also limits the co-occurrence of close relatives. Susceptibility to the same disease is frequently a consequence of shared ancestry (Gilbert and Webb, 2007), causing close relatives to suffer greater density-dependent mortality when co-present. Red oak roots are known to graft with each other more readily than with white oaks, transmitting fungal pathogens more readily among close relatives, a primary cause of oak wilt mortality in oak woodlands in the Midwest today (Juzwik, 2000; Juzwik et al., 2011). Likewise, sudden oak death causes decline in red oaks but not in white oaks (Garbelotto and Hayden, 2012). Higher abundance of specialist enemies may accrue among close relatives that co-occur, increasing pest damage (Jactel and Brockerhoff, 2007).

The widespread co-existence of oaks from different lineages (Table 2) may indicate that complementarity between them is important. In proximity, oaks of different clades are less likely to introgress (Aldrich and Cavender-Bares, 2011) or to cause mortality due to other density-dependent biotic mechanisms. Oaks share ectomycorrhizal symbionts (ECM) that enhance nutrient uptake and their presence in an oak forest community can facilitate establishment of other oak seedlings (Dickie and Reich, 2005). ECM are functionally quite distinct from arbuscular mycorrhizas (AM) that typically colonize tropical taxa—those taxa that were losing ground in the face of temperate zone expansion. ECM would have expanded with the oaks as they colonized North America, sweeping east and west of the Rocky Mountains and throughout the upper Midwest and Southeast. Co-occurrence of oak

lineages may also promote greater abundance of seed dispersal agents, such as squirrels (Steele et al., 2001) and acorn woodpeckers (McMahon et al., 2015). In addition to these effects, complementarity in the regeneration niche (Grubb, 1977) among distinct lineages, whereby direct competition for limited regeneration sites would be minimized, may have promoted coexistence of species from distinct lineages during diversification. And these mechanisms likely remain critical in ongoing assembly of the oaks. For example, 1-year seed maturation in white and live oaks compared with 2 years in red oaks causes developing ovules (seeds) to be vulnerable to climate extremes in contrasting years, leading to temporal segregation between lineages in recruitment and regeneration, thus promoting coexistence (Chesson, 1985, 2000). Mohler (1990) demonstrated higher asynchrony in masting among species pairs from different oak sections than expected.

Environmental sorting—Species within the two major lineages show similar climatic ranges and distributions, occupying a large fraction of the total climatic envelope occupied by forests in the United States (Fig. 3). The mean climatic preferences between the two clades are strikingly similar (Fig. 4), following the findings of Hipp et al. (2018), although some white oaks occur in drier habitats, particularly *Quercus gambelii*, found in the intermountain West in a region where the red oaks do not occur (Fig. 5). Additionally, a clade composed primarily of southwestern United States and northern Mexican white oaks exhibits striking differentiation in trait space from the rest of the white oaks (Fig. 4A, B), accompanied by *Q. emoryi* Torr. and *Q. hypoleucoides* A.Camus (Fig. 4A) (Schwilk et al., 2013; Fallon and Cavender-Bares, 2018), two oaks from the predominantly Mexican red oak clade. Evolutionary divergence and convergence in leaf function likely drives species current distributions along hydrologic, edaphic, and fire gradients (Cavender-Bares and Holbrook, 2001; Schwilk et al., 2013; Fallon and Cavender-Bares, 2018). For example, leaf dissection, or the perimeter × leaf length per area (PLA) in oaks varies with mean rainfall during the growing season across a range of species (Kaproth and Cavender-Bares, 2016). Thus, convergence in function (Fig. 4) likely drives co-occurrence of distantly related oaks.

Species within *Virentes* and *Protobalanus*, however, show physiological limitations and are confined to warm regions. Limits to chilling and freezing tolerance within the *Virentes* have been previously documented (Cavender-Bares and Holbrook, 2001; Cavender-Bares, 2007; Koehler et al., 2012; Cavender-Bares et al., 2015). *Protobalanus* appears to have similar limitations in California (see Ortego et al., 2015).

Leaf traits of oak taxa are highly clustered in the East and West, but overdispersed or showing no pattern on the West Coast. High SLA and PLA values are found in oaks that occur in all regions of the oak climatic envelope; however, most cold-adapted species in the upper Midwest and Northeast have high values, given that they are all deciduous and tend to have large, lobed leaves. In the Southeast, species with higher values tend to occur in more fertile, resource-rich environments, perhaps because they have shorter lifespans and are on the resource-acquisitive end of the leaf economic spectrum (Wright et al., 2004; Reich, 2014; Cavender-Bares et al., 2004b).

Sorting may operate differently in the far western geodivision. Of the eight oak tree species considered by the USFS in Pacific lowland mixed forest, *Q. agrifolia*, *Q. kelloggii*, *Q. wislizeni* (red oaks), *Q. douglasii*, *Q. lobata*, *Q. garryana*, *Q. engelmannii* (white oaks), and *Q. chrysolepis* (golden cup oak), a striking range of leaf shapes and functional trait values are represented within the red oaks and within the white and golden cup oaks. In mediterranean climates, timing of

rainfall relative to warm temperatures is offset. Specific leaf area and PLA tend to be coupled to leaf habit (evergreenness or deciduousness) and to fast vs. slow leaf economic spectrum strategies (Wright et al., 2004; Reich, 2014). Both strategies may have fitness benefits in the face of alternating stress factors and may thus be equivalently selected for by the environment. Deciduousness may be beneficial for avoiding physiological limitations due to seasonally cool temperatures and reduced photoperiod in winter months (Axelrod, 1966), while evergreenness, associated with small leaf size and low specific leaf area, should have lower boundary layer resistance allowing more rapid cooling (Givnish and Vermeij, 1976), prevention of water loss, and increased photoprotection in the face of high temperatures and drought stress in the summer months. Co-presence of contrasting leaf types may promote complementary resource acquisition, if different leaf habits represent alternative strategies for resource acquisition and result in reduced overlap in resource uptake.

A general pattern of trait clustering in the East is consistent with ecophysiological studies of oaks in this region. Co-occurring red and white oaks in the eastern pine barrens showed very similar SLA values and leaf nutrient contents, as well as indistinguishable water-use and nutrient-use efficiencies (Renninger et al., 2014), even though *Q. montana* (a white oak) was more conservative in water use per leaf area than *Q. velutina* (a red oak) (Renninger et al., 2014). Maximum stem and leaf specific hydraulic conductance (Cavender-Bares and Holbrook, 2001), gas exchange and leaf trait values (Cavender-Bares et al., 2004b) of co-occurring red and white oaks in northern central Florida were very similar to each other, although the white oaks tend to have narrower vessel diameters (Cavender-Bares et al., 2004b). Three oak species that frequently co-occur in some parts of the southeastern United States, *Quercus margarettae*, *Q. laevis* Walter, and *Q. incana*, had similar photosynthetic rates, water-use efficiency, and nitrogen content of leaves, despite differences in predawn and midday water potential and leaf phosphorus content (Donovan et al., 2000). All three species are generally considered drought avoiders.

Spatial scale—The most interesting trends in spatial scale occur in the phylogenetic structure of communities with increasing grain size. In the East and West, communities are overdispersed or tend toward overdispersion at the smallest grain size but become randomly structured or phylogenetically clustered at larger grain sizes. Interspecific interactions, including competition for resources, density-dependent vulnerability to enemies, are most likely to be relevant at small grain sizes. At larger grain sizes, such interactions are less likely to be important in structuring communities, potentially causing overdispersion to fade (Box 1: Fig. 1E, F). In the Far West, oak forest communities are phylogenetically overdispersed, regardless of grain size or spatial extent. Consistent overdispersion in the Far West may be a consequence of lower oak species richness. Gradients in climate are more pronounced in the East, and the geography of speciation, resulting in many species of the same clade within a particular climatic regime, may contribute to some degree of phylogenetic clustering, particularly at the largest grain sizes. The edaphic variation, elevation gradients, and microtopographic variation in the Southeast and Appalachian Mountain range may have promoted speciation and population expansions. The unglaciated southeastern region may also have served as a refugial region reducing extinction during glacial periods (Soltis et al., 2006). As a consequence, assemblages of the Southeast, particularly at larger grain sizes, contain more species from each major lineage than in other regions of the United States.

Linking biogeographic history to current oak diversity and abundance—The phylogenetically overdispersed oak communities we observe today, and which comprise an important fraction of the forest biomass in North America, can be understood as a consequence of lineage diversification in the deep past (30+ Ma) and associated trait diversification. The coexistence of distant relatives likely has far-reaching consequences for understanding current diversity and abundance as well as for understanding past colonization of the continent. The fact that adaptive radiation into every habitat in every geographic region was able to occur in parallel may be grounded in the ecology and life history of the oaks. Complementarity of distinct clades likely accounts for sustained resource capture permitting long-term coexistence. Reduced density-dependent mortality when distinct clades are interspersed may have allowed more species to be packed together during the early phases of colonization and diversification, just as it may today. Lack of introgression between distant relatives would have prevented merging of populations. As a consequence, more oak species could colonize and occupy a given habitat than under an allopatric diversification scenario. Intriguingly, some amount of introgression among closely related oaks may have been critical to diversification by promoting rapid adaptation as oaks expanded southward, despite long generation times (Gailing and Curtu, 2014; Cannon and Lerdau, 2015; Cannon and Scher, 2017). Introgression appears to have enabled range expansion in European white oaks (Petit et al., 2003) and North American *Populus* L. (Suarez-Gonzalez et al., 2018). The accumulation of high diversity and abundance of oaks through the process of sympatric and parallel adaptive radiation (Hipp et al., 2018) promoted by a series of ecological complementarity mechanisms throughout the most dynamic phases of speciation may have preempted expansion of other lineages. Thus, the early arrival and rapid diversification of the oaks in the expanding temperate zone during a time of changing climate may represent an evolutionary legacy effect (Cavender-Bares et al., 2016a) that established the dominance and diversity of the oaks in North America. If we were to replay the tape of life, invoking Gould's metaphor (Gould, 1989), without the right conditions that allowed the oaks to colonize, radiate in parallel and expand, other tree lineages might now be inhabiting the continent. The expansion and dominance of the oaks may have left an important legacy on north temperate forest ecosystems not necessarily predictable from environmental factors. In the face of widespread disturbance, exotic diseases, and pests (Oak et al., 2004; Karel and Man, 2015), we may see declines in these forests, which may not rebound to the same oak diversity or abundance.

We close by emphasizing that the phylogenetic and trait structure of communities has many potential causes that operate at different time scales and vary in importance. We have used the oaks as a case study to illustrate the insights gained by an integrative examination of the diversification process with the ecological mechanisms of community assembly. Ultimately, phylogenetic and functional patterns in communities tell us much more about community assembly when examined in concert with the biogeographic and evolutionary history that led to them.

ACKNOWLEDGEMENTS

DATA ACCESSIBILITY

Plot data, functional trait data, and the dated phylogeny are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j4sf2.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

LITERATURE CITED

Ackerly, D. D. 2003. Community assembly, niche conservatism and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: S165–S184.

Ackerly, D. D. 2009. Evolution, origin and age of lineages in the Californian and Mediterranean floras. *Journal of Biogeography* 36: 1221–1233.

Aldrich, P. R., and J. Cavender-Bares. 2011. Genomics and breeding of oaks and their slightly less-domesticated wild oak relatives. *In* C. Kole [ed.], Wealth of wild species: genetic, genomic and breeding resources, 89–130. Springer-Verlag, NY, NY, USA.

Alsenz, H., J. Regnery, S. Ashckenazi-Polivoda, A. Meilijson, L. Ron-Yankovich, S. Abramovich, P. Illner, et al. 2013. Sea surface temperature record of a Late Cretaceous tropical Southern Tethys upwelling system. *Palaeogeography, Palaeoclimatology, Palaeoecology* 392: 350–358.

Axelrod, D. I. 1966. Origin of deciduous and evergreen habits in temperate forests. *Evolution* 20: 1–15.

Barak, R. S., A. L. Hipp, J. Cavender-Bares, W. D. Pearse, S. C. Hotchkiss, E. A. Lynch, J. C. Callaway, et al. 2016. Taking the long view: integrating recorded, archeological, paleoecological, and evolutionary data into ecological restoration. *International Journal of Plant Sciences* 177: 90–102.

Baraloto, C., F. Morneau, D. Bonal, L. Blanc, and B. Ferry. 2007. Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology* 88: 478–489.

Barnes, R. 2016. dggridR: discrete global grids for R. Available at https://cran.r-project.org/web/packages/dggridR/vignettes/dggridR.html.

Becerra, J. X. 2005. Timing the origin and expansion of the Mexican tropical dry forest. *Proceedings of the National Academy of Sciences, USA* 102: 10919–10923.

Brunbjerg, A. K., J. Cavender-Bares, W. L. Eiserhardt, R. Ejrnæs, L. W. Aarssen, H. L. Buckley, E. Forey, et al. 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. *Journal of Plant Ecology* 7: 101–114.

Butler, M., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *American Naturalist* 164: 683–695.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079–1087.

Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *Plos One* 4: e5695.

Cannon, C. H., and M. Lerdau. 2015. Variable mating behaviors and the maintenance of tropical biodiversity. *Frontiers in Genetics* 6: 183.

Cannon, C. H., and C. L. Scher. 2017. Exploring the potential of gametic reconstruction of parental genotypes by F1 hybrids as a bridge for rapid introgression. *Genome* 60: 713–719.

Cavender-Bares, J. 2007. Chilling and freezing stress in live oaks (*Quercus* section *Virentes*): intra- and interspecific variation in PS II sensitivity corresponds to latitude of origin. *Photosynthesis Research* 94: 437–453.

Cavender-Bares, J. 2016. Diversity, distribution and ecosystem services of the North American oaks. *International Oaks* 27: 37–49.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004b. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163: 823–843.

Cavender-Bares, J., D. D. Ackerly, S. E. Hobbie, and P. A. Townsend. 2016. Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. *Annual Review of Ecology, Evolution, and Systematics* 47: 433–462.

Cavender-Bares, J., and N. Cavender. 2011. Phylogenetic structure of plant communities provides guidelines for restoration. *In* S. Greipsson [ed.], Restoration ecology, 119–130. Jones & Bartlett Learning, Sudbury, MA, USA.

Cavender-Bares, J., A. González-Rodríguez, D. A. R. Eaton, A. A. L. Hipp, A. Beulke, and P. S. Manos. 2015. Phylogeny and biogeography of the American live oaks (*Quercus* subsection *Virentes*): a genomic and population genetics approach. *Molecular Ecology* 24: 3668–3687.

Cavender-Bares, J., and N. M. Holbrook. 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. *Plant Cell and Environment* 24: 1243–1256.

Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87: S109–S122.

Cavender-Bares, J., K. Kitajima, and F. Bazzaz. 2004a. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635–662.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.

Cavender-Bares, J., and A. Wilczek. 2003. Integrating micro- and macroevolutionary processes in community ecology. *Ecology* 84: 592–597.

Chabot, B. F., and D. Hicks. 1982. The ecology of leaf life spans. *Annual Review of Ecology and Systematics* 13: 329–359.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28: 263–287.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Clavel, J., G. Escarguel, and G. Merceron. 2015. mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution* 6: 1311–1319.

Cooper, N., J. Rodríguez, and A. Purvis. 2008. A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proceedings of the Royal Society, B, Biological Sciences* 275: 2031–2037.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Crepet, W. L. 1989. History and implications of the early North American fossil record of Fagaceae. *In* P. R. Crane and S. Blackmore [eds.], Evolution,

systematics, and fossil history of the Hamamelidae, vol. 2, Systematics Association Special Volume No. 40B, 45–66. Clarendon Press, Oxford, UK.

Crisp, M. D., M. T. K. Arroyo, L. G. Cook, M. A. Gandolfo, and G. J. Jordan. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458: 754–756.

Davies, T. J., S. Meiri, T. G. Barraclough, and J. L. Gittleman. 2007. Species coexistence and character divergence across carnivores. *Ecology Letters* 10: 146–152.

Dickie, I. A., and P. B. Reich. 2005. Ectomycorrhizal fungal communities at forest edges. *Journal of Ecology* 93: 244–255.

Donovan, L. A., J. B. West, and K. W. McLeod. 2000. *Quercus* species differ in water and nutrient characteristics in a resource-limited fall-line sandhill habitat. *Tree Physiology* 20: 929–936.

Eaton, D., A. González-Rodríguez, A. Hipp, and J. Cavender-Bares. 2015. Historical introgression among the American live oaks and the comparative nature of tests for introgression. *Evolution* 69: 2587–2601.

Eaton, D. A. R., C. B. Fenster, J. Hereford, S.-Q. Huang, and R. H. Ree. 2012. Phylogenetic and ecological patterns of floral diversity predict reproductive interference in a biodiversity hotspot. *Ecology* 93: S182–S194.

Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, and S. A. Smith. 2010. The Origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science* 328: 587–591.

Emerson, B. C., and R. G. Gillespie. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* 23: 619–630.

Fallon, B., and J. Cavender-Bares. 2018. Leaf-level trade–offs between drought avoidance and desiccation recovery drive elevation stratification in arid oaks. *Ecosphere*. In press.

Fine, P. V. A. 2015. Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* 46: 369–392.

Forster, A., S. Schouten, M. Baas, and J. S. Sinninghe Damsté. 2007. Mid-Cretaceous (Albian–Santonian) sea surface temperature record of the tropical Atlantic Ocean. *Geology* 35: 919–922.

Gailing, O., and A. L. Curtu. 2014. Interspecific gene flow and maintenance of species integrity in oaks. *Annals of Forest Research* 57: 5–18.

Garbelotto, M., and K. J. Hayden. 2012. Sudden oak death: interactions of the exotic oomycete *Phytophthora ramorum* with naïve North American hosts. *Eucaryotic Cell* 11: 1313–1323.

Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.

Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences, USA* 104: 4979–4983.

Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303: 356–359.

Givnish, T. J., K. C. Millam, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, et al. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society, B, Biological Sciences* 276: 407–416.

Givnish, T. J., and G. J. Vermeij. 1976. Size and shapes of liane leaves. *American Naturalist* 110: 743–778.

Gould, S. J. 1989. Wonderful life: the Burgess Shale and the nature of history. W. W. Norton, NY, NY, USA.

Graham, A. 1999. Late Cretaceous and Cenozoic history of North American vegetation north of Mexico. Oxford University Press, NY, NY, USA.

Graham, A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. *American Journal of Botany* 98: 336–351.

Green, P. 1995. Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. *Biometrika* 82: 711–732.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.

Hansen, T. F. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51: 1341–1351.

Hawkins, B. A., M. Rueda, T. F. Rangel, R. Field, and J. E. A. F. Diniz-Filho. 2014. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. *Journal of Biogeography* 41: 23–38.

Helmus, M. R. 2007. Separating the determinants of phylogenetic community structure. *Ecology Letters* 10: 917–925.

Hernández-Hernández, T., J. W. Brown, B. O. Schlumpberger, L. E. Eguiarte, and S. Magallón. 2014. Beyond aridification: multiple explanations for the elevated diversification of cacti in the New World Succulent Biome. *New Phytologist* 202: 1382–1397.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hipp, A. L., D. J. Larkin, R. S. Barak, M. L. Bowles, M. W. Cadotte, S. K. Jacobi, E. Lonsdorf, et al. 2015. Phylogeny in the service of ecological restoration. *American Journal of Botany* 102: 647–648.

Hipp, A. L., P. S. Manos, González-Rodríguez, M. Hahn, M. Kaproth, J. D. McVay, S. V. Avalos, and J. Cavender-Bares. 2018. Sympatric parallel diversification of major oak clades in the Americas and the origins of Mexican species diversity. *New Phytologist* 217 439–452.

Horner-Devine, M. C., and B. J. M. Bohannan. 2006. Phylogenetic clustering and overdispersion in bacterial communities. *Ecology* 87: S100–S108.

Jactel, H., and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10: 835–848.

Juzwik, J. 2000. An oak wilt primer. *International Oaks* 11: 14–20.

Juzwik, J., D. N. Appel, W. L. MacDonald, and S. Burks. 2011. Challenges and success in managing oak wilt in the United States. *Plant Disease* 95: 888–900.

Kaproth, M., and J. Cavender-Bares. 2016. Drought tolerance and climatic distributions of the American oaks. *International Oaks* 27: 49–60.

Karel, T. H., and G. Man [compilers]. 2015. Major forest insect and disease conditions in the United States. U.S. Department of Agriculture U. S. Forest Service, Washington, D.C., USA. Available at http://www.fs.fed.us/foresthealth/publications/ConditionsReport_2015.pdf [accessed 01 Month 2017].

Keddy, P., and E. Weiher. 1999. Introduction: The scope and goals of research on assembly rules. *In* E. Weiher and P. Keddy [eds.], Ecological assembly rules: perspectives, advances, retreats, 1–22. Cambridge University Press, Cambridge, UK.

Keller, I., C. E. Wagner, L. Greuter, S. Mwaiko, O. M. Selz, A. Sivasundar, S. Wittwer, and O. Seehausen. 2013. Population genomic signatures of divergent adaptation, gene flow and hybrid speciation in the rapid radiation of Lake Victoria cichlid fishes. *Molecular Ecology* 22: 2848–2863.

Kembel, S. W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12: 949–960.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.

Kikuzawa, K. 1995. The basis for variation in leaf longevity of plants. *Vegetatio* 121: 89–100.

Koehler, K., A. Center, and J. Cavender-Bares. 2012. Evidence for a freezing tolerance–growth rate trade-off in the live oaks (*Quercus* series *Virentes*) across the tropical–temperate divide. *New Phytologist* 193: 730–744.

Kozak, K. H., A. A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: Desmognathus). *Evolution* 59: 2000–2016.

Kozak, K. H., R. W. Mendyk, and J. J. Wiens. 2009. Can parallel diversification occur in sympatry? Repeated patterns of body size evolutin in coexisting clades of North American salamanders. *Evolution* 63: 1769–1784.

Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80: 401–422.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015a. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29: 592–599.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170: 271–283.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015b. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences, USA* 112: 797–802.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an amazonian forest. *Science* 322: 580–582.

Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter, et al. 2015. Plant functional traits have globally consistent effects on competition. *Nature* 529: 204.

Kunstler, G., S. Lavergne, B. Courbaud, W. Thuiller, G. Vieilledent, N. E. Zimmermann, J. Kattge, and D. A. Coomes. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters* 15: 831–840.

Laliberté, E., A. Paquette, P. Legendre, and A. Bouchard. 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159: 377–388.

Larcombe, M. J., B. Holland, D. A. Steane, R. C. Jones, D. Nicolle, R. E. Vaillancourt, and B. M. Potts. 2015. Patterns of reproductive isolation in *Eucalyptus*—a phylogenetic perspective. *Molecular Biology and Evolution* 32: 1833–1846.

Lasky, J. R., M. Uriarte, V. K. Boukili, and R. L. Chazdon. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences, USA* 111: 5616–5621.

Lebrija-Trejos, E., E. A. Pérez-García, J. A. Meave, F. Bongers, and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91: 386–398.

Lessard, J.-P., B. G. Weinstein, M. K. Borregaard, K. A. Marske, D. R. Martin, J. A. McGuire, J. L. Parra, et al. 2015. Process-based species pools reveal the hidden signature of biotic interactions amid the influence of temperature filtering. *American Naturalist* 187: 75–88.

Levin, D. A. 2006. The spatial sorting of ecological species: Ghost of competition or of hybridization past? *Systematic Botany* 31: 8–12.

Lind, E. M., J. B. Vincent, G. D. Weiblen, J. M. Cavender-Bares, and E. T. Borer. 2015. Trophic phylogenetics: evolutionary influences on body size, feeding, and species associations in grassland arthropods. *Ecology* 96: 998–1009.

Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology & Evolution* 18: 220–227.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118.

Losos, J. B., M. Leal, R. E. Glor, K. de Queiroz, P. E. Hertz, L. R. Schettino, A. C. Lara, et al. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424: 542–545.

Manos, P. S., J. J. Doyle, and K. C. Nixon. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* 12: 333–349.

Manos, P. S., and A. M. Stanford. 2001. The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Sciences* 162: S77–S93.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McMahon, D. E., I. S. Pearse, W. D. Koenig, and E. L. Walters. 2015. Tree community shifts and Acorn Woodpecker population increases over three decades in a Californian oak woodland. *Canadian Journal of Forest Research* 45: 1113–1120.

McVay, J. D., D. Hauser, A. L. Hipp, and P. S. Manos. 2017. Phylogenomics reveals a complex evolutionary history of lobed-leaf white oaks in Western North America. *Genome* 60: 733–742.

Mohler, C. L. 1990. Co-occurrence of oak subgenera: implications for niche differentiation. *Bulletin of the Torrey Botanical Club* 117: 247–255.

Mouillot, D., A. Simkova, S. Morand, and R. Poulin. 2005. Parasite species coexistence and limiting similarity: a multiscale look at phylogenetic, functional and reproductive distances. *Oecologia* 146: 269–278.

Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76: 521–547.

Nixon, K. C. 1997. *Quercus* Linnaeus. *In* Flora of North America Editorial Committee [ed.], Flora of North America north of Mexico, vol. 3, 431–506. Oxford University Press, NY, NY, USA.

Oak, S. W., J. R. Steinman, D. A. Starkey, and E. K. Yockey. 2004. Assessing oak decline incidence and distribution in the southern U.S. using forest inventory and analysis data. In: Spetich, M.A. (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability, Gen. Tech. Rep. SRS-73, Fayetteville, AR, October 7–10, 2002. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 236–242.

Ortego, J., P. F. Gugger, and V. L. Sork. 2015. Climatically stable landscapes predict patterns of genetic structure and admixture in the Californian canyon live oak. *Journal of Biogeography* 42: 328–338.

Pearse, I. S., and A. L. Hipp. 2012. Global patterns of leaf defenses in oak species. *Evolution* 66: 2272–2286.

Pennington, R. T., Q. C. B. Cronk, and J. A. Richardson. 2004. Introduction and synthesis: plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 359: 1455–1464.

Pennington, R. T., M. Lavin, and A. Oliveira-Filho. 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics* 40: 437–457.

Petit, R. J., C. Bodenes, A. Ducousso, G. Roussel, and A. Kremer. 2003. Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151–164.

Pollock, L. J., M. J. Bayly, and P. A. Vesk. 2015. The roles of ecological and evolutionary processes in plant community assembly: the environment, hybridization, and introgression influence co-occurrence of *Eucalyptus*. *American Naturalist* 185: 784–796.

Prinzing, A., R. Reiffers, W. G. Braakhekke, S. M. Hennekens, O. Tackenberg, W. A. Ozinga, J. H. J. Schaminee, and J. M. van Groenendael. 2008. Less lineages—more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecology Letters* 11: 809–819.

Prothero, D. R. 2009. Tertiary history. *In* V. Cilek [ed.], vol. II, Earth system: history and natural variability. Encyclopedia of Life Support Systems [EOLSS] Publications, Oxford, UK.

Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Renninger, H. J., N. Carlo, K. L. Clark, and K. V. R. Schäfer. 2014. Physiological strategies of co-occurring oaks in a water- and nutrient-limited ecosystem. *Tree Physiology* 34: 159–173.

Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7: 1–15.

Ricklefs, R. E. 2007. History and diversity: Explorations at the intersection of ecology and evolution. *American Naturalist* 170: S56–S70.

Sack, L., P. D. Cowan, N. Jaikumar, and N. M. Holbrook. 2003. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant Cell and Environment* 26: 1343–1356.

Sack, L., and C. Scoffoni. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* 198: 983–1000.

Savage, J., and J. Cavender-Bares. 2012. Habitat specialization and the role of trait lability in structuring diverse willow (genus *Salix*) communities. *Ecology* 93: S138–S150.

Schluter, D. 1996. Ecological causes of adaptive radiation. *American Naturalist* 148, supplement: S40–S64.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, NY, NY, USA.

Schwilk, D. W., M. S. Gaetani, and H. M. Poulos. 2013. Oak bark allometry and fire survival strategies in the Chihuahuan desert sky islands, Texas. *USA. PLOS One* 8: e79285.

Simpson, G. G. 1953. The major features of evolution. Columbia University Press, NY, NY, USA.

Slingsby, J. A., and G. A. Verboom. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *American Naturalist* 168: 14–27.

Soltis, D., A. Morris, J. S. McLachlan, P. S. Manos, and P. S. Soltis. 2006. Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology* 15: 4261–4293.

Souza-Neto, A. C., M. V. Cianciaruso, and R. G. Collevatti. 2016. Habitat shifts shaping the diversity of a biodiversity hotspot through time: insights from the phylogenetic structure of Caesalpinioideae in the Brazilian Cerrado. *Journal of Biogeography* 43: 340–350.

Steele, M. A., P. D. Smallwood, A. Spunar, and E. Nelsen. 2001. The proximate basis of the oak dispersal syndrome: detection of seed dormancy by rodents. *American Zoologist* 41: 852–864.

Stoks, R., and M. A. McPeek. 2006. A tale of two diversifications: reciprocal habitat shifts to fill ecological space along the pond permanence gradient. *American Naturalist* 168: S50–S72.

Suarez-Gonzalez, A., C. A. Hefer, C. Lexer, C. J. Douglas, and Q. C. B. Cronk. 2018. Introgression from *Populus balsamifera* underlies adaptively significant variation and range boundaries in *P. trichocarpa*. *New Phytologist* 217: 416–427.

Swenson, N. G., B. J. Enquist, J. Pither, A. J. Kerkhoff, B. Boyle, M. D. Weiser, J. J. Elser, et al. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* 21: 798–808.

Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology* 87: 2418–2424.

Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770–1780.

Thibault, N., R. Harlou, N. H. Schovsbo, L. Stemmerik, and F. Surlyk. 2015. Late Cretaceous (Late Campanian–Maastrichtian) sea surface temperature record of the Boreal Chalk Sea. *Climate of the Past* 11: 5049–5071.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice. Springer, NY, NY, USA.

Tyerman, J. G., M. Bertrand, C. C. Spencer, and M. Doebeli. 2008. Experimental demonstration of ecological character displacement. *BMC Evolutionary Biology* 8: https://doi.org/10.1186/1471-2148-1188-1134.

Uyeda, J. C., and L. J. Harmon. 2014. A novel Bayesian method for inferring and interpreting the dynamics of adaptive landscapes from phylogenetic comparative data. *Systematic Biology* 63: 902–918.

Valiente-Banuet, A., and M. Verdú. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10: 1029–1036.

Vamosi, J. C., and S. M. Vamosi. 2007. Body size, rarity, and phylogenetic community structure: insights from diving beetle assemblages of Alberta. *Diversity and Distributions* 13: 1–10.

Van Der Meer, D. G., R. E. Zeebe, D. J. J. van Hinsbergen, A. Sluijs, W. Spakman, and T. H. Torsvik. 2014. Plate tectonic controls on atmospheric CO_2 levels since the Triassic. *Proceedings of the National Academy of Sciences, USA* 111: 4380–4385.

Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25: 233–239.

Villalobos, F., T. F. Rangel, and J. A. F. Diniz-Filho. 2013. Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. *Proceedings of the Royal Society, B, Biological Sciences* 280: 20122570.

Wainwright, P., M. E. Alfar, D. I. Bolnick, and C. D. Hulsey. 2005. Many-to-one mapping of form to function: A general principle in organismal design? *Integrative and Comparative Biology* 45: 256–262.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *American Naturalist* 156: 145–155.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5: 181.

Webb, C. O., G. S. Gilbert, and M. J. Donoghue. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a bornean rain forest. *Ecology* 87: S123–S131.

Wei, X., J. A. Savage, C. E. Riggs, and J. Cavender-Bares. 2017. An experimental test of fitness variation across a hydrologic gradient predicts willow and poplar species distributions. *Ecology* 98: 1311–1323.

Weiher, E., and P. Keddy. 1999a. Assembly rules as general constraints on community composition. *In* E. Weiher and P. Keddy [eds.], Ecological assembly rules: perspectives, advances, retreats, 251–271. Cambridge University Press, Cambridge, UK.

Weiher, E., and P. Keddy. 1999b. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK.

Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography* 33: 565–577.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Yan, C., Y. Xie, X. Li, M. Holyoak, and Z. Zhang. 2016. Species co-occurrence and phylogenetic structure of terrestrial vertebrates at regional scales. *Global Ecology and Biogeography* 25: 455–463.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.