Received: 2 June 2021 | Accepted: 17 October 2021

DOI: 10.1111/1365-2435.13964

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Adaptive variation among oaks in wood anatomical properties is shaped by climate of origin and shows limited plasticity across environments

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Funding information
NSF DEB, Grant/Award Number: 1146380; U.S.NSF DBI, Grant/Award Number: 2021898

Handling Editor: Mark Tjoelker

Abstract

1. Climate is a major evolutionary force in driving adaptive differentiation and plasticity in plant function. Xylem anatomy and hydraulic architecture are critical to water use, growth and responses of trees to drought and thus important in delimiting their ecological niches. How wood properties have been shaped through evolution by their climatic origins and the importance of plasticity for species persistence remain open questions critical to understanding plant responses to changing climate.
2. We measured 11 wood anatomical traits for 18 *Quercus* (oak) species in arboreta that span contrasting climates (California-US, southwestern France and central England). We investigated coordinate evolution of xylem anatomical properties with climatic niche and intraspecific variation in relation to growth environment.
3. Species originating from climates with drier summers had traits associated with higher resistance to drought—higher density of vasicentric tracheids (VT), lower vessel hydraulic diameter (D_{mh}) and lower hydraulic conductivity. Species that evolved in climates with drier, hotter summers or colder winters had higher numbers of VT than those from mesic climates, supporting hypotheses that VT are critical for water transport during drought. We found limited intraspecific variation in xylem traits associated with growth environment—only four traits (pit fraction, VT, vessel density and D_{mh})—differed among gardens.
4. Xylem traits showed high lability across the phylogeny, consistent with evidence for parallel sympatric adaptive radiation and global diversification of the oaks. Our results provide evidence for the physiological mechanisms that underlie adaptation to changing environments and responses to climate change.

KEYWORDS

climatic niche, coordinate evolution, phylogenetic signal, plasticity, *Quercus*, vasicentric tracheid, xylem anatomy

1 | INTRODUCTION

Climate is a primary factor controlling the evolution and broad-scale distribution of plants and accounts for major changes in species composition across the Earth (Anderegg et al., 2016; Thuiller et al., 2008). On a global scale, variation in temperature and in the timing and amount of precipitation establishes contrasting selection pressures that have led to local adaptation (Browne et al., 2019; Etterson & Shaw, 2001; van Boheemen et al., 2019) and adaptive differentiation among populations (Ågren & Schemske, 2012; Browne et al., 2019; Cavender-Bares & Ramírez-Valiente, 2017; De Kort et al., 2014) and species (Carlson et al., 2011; Fallon & Cavender-Bares, 2018; Halbritter et al., 2018; Mitchell et al., 2018). Consequently, species' climatic niches often predict genetically based physiological tolerances to stress resulting in critical life-history trade-offs that confer fitness advantages in different environments (Koehler et al., 2012; Lancaster et al., 2017; Savage & Cavender-Bares, 2013). Determining how climate of origin influences the physiological limits of species, and the nature of variation among species is key to understanding species responses to climate change and providing guidelines for conservation (Cavender-Bares & Ramírez-Valiente, 2017; Donohue, 2003; Palacio-López et al., 2015).

In long-lived species, plasticity is an important means of surviving spatial and temporal environmental variation, by allowing plants with a single genotype to change their expressed phenotype in different environments (Parmesan, 2006), and may be more critical than local adaptation in tolerating seasonal stress (Cavender-Bares & Ramírez-Valiente, 2017; Henn et al., 2018). Since phenotypic plasticity influences environmental tolerance, different plastic responses may contribute to differences in the range of habitats that species inhabit (Ackerly et al., 2000; Matesanz et al., 2010; Razgour et al., 2019). Understanding how plant species will respond to these new scenarios in a global change context and what mechanisms will be involved in the process is fundamental to managing plant diversity (Bazzaz & Bazzaz, 1996; Parmesan, 2006). Furthermore, distinguishing between plasticity and genetically based variation has important implications for understanding range limits and how plants respond to changing environments.

The study of local adaptation and plastic differentiation encompasses the characterization of phenotypes through functional traits. Species' traits are formed over millions of years of evolution, and reflect legacies of their biogeographical and environmental origins but also evolve in response to changing environments (Cavender-Bares, 2019; Leibold & Chase, 2017). Thus, functional traits are an important mechanistic link by which phylogenetic and biogeographical history influence ecosystem function (Cavender-Bares, 2019). Xylem anatomical and hydraulic traits—linked to the tolerance of temperature variation and water availability—play a key role in species distributions and in delimiting their ecological niches across climatic gradients in many biomes (Choat et al., 2012; Cosme et al., 2017; Fontes & Cavender-Bares, 2020; Fontes et al., 2020; Robert et al., 2017; Zanne et al., 2014). However, how wood properties have been shaped through evolution by their climatic origins and the influence of plasticity in the xylem traits remain open questions critical for predicting the sensitivity of species to climate shifts and how species may continue evolving under future climate change (Hoffmann & Sgro, 2011). Furthermore, there are still many anatomical properties of the xylem that are poorly explored (e.g. Pratt et al., 2021). For example, the adaptive significance of vasicentric tracheids—tiny conduits adjacent to vessels—hypothesized to connect vessels laterally and provide enough conductive tissue to maintain sufficient water flow to support transpiration during unfavourable periods (Carlquist, 1985; Pan & Tyree, 2019; Pratt et al., 2015).

Conduit diameter and density, on the other hand, are perhaps the two most widely measured anatomical properties of trees. These two traits are inversely related, and diameter is strongly associated with hydraulic efficiency and vulnerability, particularly because of the fourth-power relationship between hydraulic conductivity and conduit diameter (Percolla et al., 2021; Sperry et al., 2006; Tyree & Sperry, 1989). By contrast, vessel density is negatively associated with hydraulic efficiency, but positively associated with embolism resistance (Pratt & Jacobsen, 2017). Furthermore, these traits differ along climatic gradients (e.g. Borghetti et al., 2017; Fontes et al., 2020; Villar-Salvador et al., 1997). For instance, regions with high water availability usually promote the formation of large vessels which fosters a higher efficiency in water movement through plants and a fast resource acquisition strategy (Reich, 2014; Tyree & Zimmermann, 2013). Also, very small vessels together with high vessel density are associated with drier environments in *Eucalyptus* spp. (e.g. Pfautsch et al., 2016). Vessel vulnerability is also dependent on pit membrane properties (Choat et al., 2008; Jacobsen et al., 2007; Li et al., 2016). Pits have a central role in controlling the spread of air emboli in conduits by preventing the movement of gas between conduits; however, the structural variability of inter-vessel pits is not well documented.

The genus *Quercus* compromises more than 430 species and occupies contrasting habitats around the globe (Cavender-Bares, 2019). This biogeographical and taxonomic diversity has resulted in a wide range of variation in physiological and morphological traits, including very different xylem structures (Gil-Pelegrín et al., 2017; Sancho-Knapik et al., 2020). Because of their economic, cultural and ecological importance, oaks have been focal group for the development of methods and hypotheses related to tree structure and function (e.g. Cavender-Bares, 2019; Pratt et al., 2020; Robert et al., 2017; Skelton et al., 2021). Yet, we are still far from understanding the various mechanisms by which oaks can maintain function during unfavourable periods. Also, the associations between functional strategies and climatic niches together with the roles of phenotypic plasticity in the evolution of trait coordination are still not well understood. Thus, this study advances prior work by analysing how evolutionary history, climate and phenotypic plasticity influence the anatomical properties of wood and their effect on hydraulic functioning and water regulation within the oaks.

Here we investigated interspecific and intraspecific variation in 11 xylem traits in 18 species of *Quercus* across three Botanical gardens located around the globe (California-US, central England

and southwestern France). Specifically, we asked four related questions: (H1) How conserved are wood anatomical properties across the phylogeny? Do xylem traits differ among the major oak lineages (sections)? (H2) Do wood anatomical properties show correlated evolution associated with species' climatic niche? Are these patterns consistent across scales (e.g. across and within a single garden)? (H3) How do the xylem anatomical traits within species vary across gardens under different climatic conditions reflecting trait plasticity? In other words, how does environmental variation shift wood anatomical traits? (H4) How do the combined influences of climatic origin and local growth environment influence wood properties?

Since different lineages of oak species occur in the same climates and species from the same major clades are found in many different environments and contrasting climatic regimes, we expected wood properties to be relatively labile in alignment with evidence of sympatric parallel adaptive radiation in the Americas (Cavender-Bares et al., 2018; Hipp et al., 2018) and widespread diversification globally (Hipp et al., 2020). We hypothesized that oaks originated in drier environments would have narrower vessels, lower vessel area and smaller pit membranes that occur with lower density within inter-conduit pit fields (i.e. lower pit fraction; Pit_F) when compared to oaks from wetter locations. Within species, we further anticipated that individuals growing in climatically drier locations would have narrower vessels, lower hydraulic conductivity smaller pit membranes with lower Pit_F, demonstrating co-gradient plasticity at species level in wood properties. However, we hypothesized that evolved (genetically based) variation among species would have a stronger influence on wood properties than plastic variation within species across climates, due to strong selective pressure for local adaptation.

2 | MATERIALS AND METHODS

2.1 | Study site

Samples were collected from three different arboretums around the globe: University of California Davis Arboretum in the United States, Sir Harold Hillier Gardens Arboretum in England and Arboretum des Pouyouleix in France. The Peter J. Shields Oak Grove at UC Davis Arboretum is located in the city of Davis-CA (38°32′01.9″N, 121°45′11.2″W) that has a Mediterranean type of climate and a mean annual temperature from 1893 to 2016 was 15.5°C and the mean annual precipitation was 445.7 mm (WRCC, 2020). The Hillier Arboretum is located 5 km northeast of the town of Romsey-Hampshire (51°00′40″N, 1°28′00″W), the climate in the region is classified as warm and temperate (the Köppen-Geiger climate classification is Cfb), mean annual temperature from 1982 to 2019 was 10.4°C and mean annual precipitation was 750 mm (Climate-Data, 2020). The Arboretum des Pouyouleix is specialized in oaks and is located in Saint-Jory-de-Chalais—Aquitaine (45°28′24.7″N, 0°53′17.4″E), the average annual minimum temperature from 2009 to 2017 varied from −9.4 to −6.7°C and the average annual maximum varied from 24°C to 30°C. Mean annual precipitation was around 917 mm (Chassé, 2017). Therefore, UC Davis Arboretum in California is the driest place (higher temperature and lower precipitation) sampled in this study, followed by England and France. More information about the climatic conditions of each garden is shown in Table S1.

2.2 | Climate characterization

To estimate species' climatic niche, we randomly sampled around 500 geographical points throughout the distribution range of each species from herbarium records available at the Global Biodiversity Information Facility (http://www.gbif.org/). To characterize the average climate for the 500 geographical points within the distribution range of each species, we used a subset of variables from the WorldClim database (http://www.worldclim.org/) that were chosen because they are important in the context of oak distribution and niche differentiation. The climatic variables selected were as follows: BIO1 (annual mean temperature), BIO2 (mean diurnal range, mean of monthly (maximum temperature – minimum temperature)), BIO3 (isothermality), BIO5 (maximum temperature of the warmest month), BIO6 (minimum temperature of the coldest month), BIO 9 (mean temperature of the driest quarter), BIO 10 (mean temperature of the warmest quarter), BIO12 (annual precipitation), BIO14 (precipitation of the driest month) and AI (aridity Index); see Ramírez-Valiente et al. (2020) and Hijmans et al. (2005) for details.

2.3 | Species selection

In this study, we sampled a total of 18 oak species of which 12 were collected in more than one garden. We sampled 15 species in California (CA), 9 in France (FR) and 7 in England (EN; Table S2). We had five species that were common to the CA and FR gardens, three to the CA and EN, another three to the FR and EN, and one that was present in all the gardens (Table S6). The species are characterized by different growth forms, leaf phenology, ecological niches and distribution ranges. We collected from three mature trees per species, grown from seeds (thus, the individuals have only been exposed to the climate of each garden), and they were all sampled from June to September of 2019. For some species, due to the sampling limitation in each garden, we were only able to collect two individuals (see Tables S6 for details on the number of individuals collected per species in each garden). All the 18 species were used to test H1 and H2. A subset of these species, including the 12 species that were sampled in more than one garden, were used to investigate H3 and H4.

2.4 | Xylem anatomy and hydraulic traits

We selected 11 xylem anatomical traits that are related to mechanical strength, sap transport and xylem vulnerability to embolism (Table 1). For the xylem anatomical traits, we collected one branch

(>30 cm) per individual (3 individuals per species), and they varied from around 1 to 3 cm in diameter and from 2 and 6 years old. Each branch was (~8 cm), placed in coin envelops and dried for at least 72 hr in a drying oven at 60°C for storage. Before we started anatomical procedures, branch samples were hydrated in DI water under vacuum for 5 min and then in the refrigerator for at least 5 days floating on water.

For cross-section analyses, each branch sample was cut in 40 μm thick sections using a sledge microtome (AO Spencer, No. 860). The cross-sections were stained in 1% Safranin O solution for 10 min and rinsed with water. Up to eight cross-sections per branch were mounted in glycerine for histological examination. We selected one cross-section per sample and used a digital camera (Zeiss Microscopy, Axiocam 305 colour) mounted on a light microscope (Olympus, BX50) to shoot photos with an APO ×20 lens of growth rings 2, 3 and 4. These growth rings were selected because for some species we were unable to sample branches older than 4 years of age and we decided to exclude year 1 since this ring is diffuse porous and unique, especially in species that produce ring porous xylem in later years (Pratt et al., 2020; Rodríguez-Zaccaro et al., 2019). Cambial age was determined by counting rings in cross-sections. Image analyses were conducted with ImageJ-Fiji4 (Schindelin et al., 2012). For images with good contrast, we performed an automated delimitation of the vessels with a threshold function in Fiji. For those with lower contrast, we manually filled the vessel areas. For each image, we measured individual vessel area (to estimate mean vessel area = VA; μm^2), vessel diameter (D) and counted the total number of vessels per unit area (vessel density = VD; $n\ \mu m^{-2}$). Vessel diameter was estimated as $D = (D_1 + D_2)/2$ (i.e. the mean diameter of an ellipse), where D_1 is the maximum vessel diameter and D_2 is the minimum vessel diameter in μm. Anything smaller than 10 μm was not considered in the vessels' analyses. We calculated three metrics of hydraulic efficiency, vessel fraction as VF = VA ×VD; the ratio between size and number of vessels, S = VA/VD; and the mean vessel hydraulic diameter (μm), $D_{mh} = (\sum D^4/n)^{1/4}$ where n is the total number of vessels in an image (Scholz et al., 2013; Zanne et al., 2010). The number of vasicentric tracheids (VT) was estimated by counting the number of VT present adjacent to vessels—tracheids that were partially within the image were also considered—in an area of 8,000 μm^2. The conductivity index (I_k) was estimated as $I_k = n \times D^4_{mh}$ (Fortunel et al., 2014). The theoretical specific conductivity (K_{theo}) was calculated using the equation of Hagen–Poiseuille:

$$K_{theo} = \left(\frac{\pi}{128\eta \times A_S}\right) \times \sum D^4 \times \rho_{water} (kg\, m^{-1}\, s^{-1}\, MPa^{-1}), \quad (1)$$

where A_s is the cross-section area of sapwood in the branch, η is the viscosity of water (1.002 × 10^{-9} MPa/s) and ρ_{water} is the density of water (998.23 kg/m^3), both at 20°C (Santiago et al., 2004; Tyree & Ewers, 1991).

For transversal analyses, each branch sample was cut in ~15 μm thick sections using a sledge microtome (AO Spencer, No. 860). Transversal sections were stained in 1% Safranin O solution for 10 min and rinsed with water. Sections were embedded in glycerine for histological examination. We used a digital camera (Zeiss Microscopy, Axiocam 305 colour) mounted on a light microscope (Olympus, BX50) to shoot pit photos with an APO ×40 lens. For each sample, 10 pits occurring next to each other were selected and pit membrane area (Pit_A) and pit membrane diameter (Pit_D) of each individual pit was measured. Pit fraction (Pit_F), which is the mean fraction of the vessel area occupied by the inter-vessel pits, was calculated as the total area of inter-vessel pit membranes within a pit field divided by the examined surface area of the vessel wall (Jacobsen et al., 2018).

2.5 | Statistical analysis

To test H1 and estimate the phylogenetic signal of wood anatomical traits, we calculated Blomberg's K (Blomberg et al., 2003) using the most recent phylogenetic tree published for the genus *Quercus* (Hipp et al., 2020). For the phylogenetic signal analyses, the data were log-transformed and the measurement error was considered for K calculations. We tested two hypotheses regarding observed K values: (a) lack of phylogenetic signal—observed K is

TABLE 1 List of 11 xylem anatomical traits measured at the branch level for this study with corresponding abbreviations and units

Traits	Abbreviation	Units
Mean vessel hydraulic diameter	D_{mh}	μm
Theoretical specific hydraulic conductivity	K_{theo}	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$
Number of vasicentric tracheid	VT	n
Conductivity index	I_k	$n\ \mu m^{-2}$
Vessel density	VD	$n\ \mu m^{-2}$
Vessel area (porosity)	VA	μm^2
Vessel fraction	VF	
Vessel size to number ratio	S	
Pit diameter	Pit_D	μm
Pit membrane area	Pit_A	μm^2
Pit fraction	Pit_F	%

not greater than would be expected if trait values for species were randomized among tips (with 1,000 randomized samples; white noise null model) and (b) consistency with Brownian motion (BM) evolution model—whether *K* significantly departed from the phylogenetic signal estimated from 1,000 simulated datasets in which BM was the evolutionary model. The code for *K* estimation can be found here: https://github.com/jesusNPL/PhyloSignal/blob/master/demon_K_test_ME.R. Phylogenetic ANOVA test and post-hoc comparisons were performed to check if wood anatomical traits were significantly different among the distinct sections—*Cerris*, *Ilex*, *Lobatae* and *Quercus* (section *Quercus* was divided into eastern and western white oaks).

To test whether the climate of origin is associated with wood anatomy properties across species (H2), we performed a forward stepwise multiple phylogenetic regression. For climatic variables that were highly correlated, we selected only one of them to be represented in the model. We removed climatic variables that were highly correlated with one another. We used a recent phylogeny of *Quercus* based on single nucleotide polymorphism obtained by ddRAD sequencing extracted from Hipp et al. (2020) that contains the 18 sampled species. The trait values were normalized by the species overall mean (individuals from all gardens were considered) and were the dependent variables in the models; the climatic variables were the explanatory variables. This method allowed us to identify the best predictor variable of species traits without the need for multiple testing (inflating type I error). We performed a PCA to summarize the climatic variables into two single axes (PC1 and PC2). In addition to the 10 climatic variables, we also used PC1 and PC2 extracted from principal component analysis (PCA) as explanatory variables. We then performed a set of phylogenetic generalized least squares (PGLS) with the best predictor climatic factors as the explanatory variables of the models and the trait values as the dependent variables. We standardized trait values by each species overall mean so variation within one trait has equal influence in the analyses as variation in any other trait.

Linear mixed-effect models, with species as a random intercept and garden + leaf phenology as a fixed factor, were used to evaluate if individuals from the 12 species sampled in the different gardens have distinct trait values (plasticity; H3). Linear mixed-effect models (species as a random intercept) were also used to determine the contribution of climate of origin and local environment (fixed factors) on trait variability (H4). We quantified the proportion of variance explained by the models with the marginal R^2 (for the fixed effects) and the conditional R^2 (for the fixed and random effects combined; Bartoń, 2019; Nakagawa & Schielzeth, 2013). To validate the linear mixed-effect models, we verified visually if residuals were homogeneous and if there were any over-influential observations, using Cook's distance (Thomas et al., 2017). We also checked for normality of the fitted coefficients of the random terms. The residual of the traits that did not meet the assumptions of a normal distribution (K_{theo} and VD) were log-transformed before analysis. For all statistical analyses, we used R v.3.4.2 with BASE packages R Core Team (2018).

3 | RESULTS

3.1 | Phylogenetic signal and trait conservatism

All the 11 xylem traits were not statistically different from the white noise null model, but significantly different from the Brownian motion model of evolution, indicating a low phylogenetic signal and a high degree of trait lability among species within the oak lineages (Figure 1; Table 2). These results are in alignment with the phylogenetic ANOVA tests (Table S7), where trait values across the sections were not significantly different ($p > 0.067$; Figure 1).

3.2 | Species climatic niche and wood anatomy properties

In the Principal Components Analyses (PCA) of the climatic variables, two axes explained 79.6% of the total variance in climatic niche across species distribution ranges. PC1 explained 53.1% of the variance and was an indicator of arid conditions. This axis was positively related (positive loadings) to aridity index (higher values = more humid conditions), annual precipitation (BIO12) and precipitation of the driest month (BIO14) and negatively related to minimum temperature of the coldest month (BIO6), temperature diurnal range (BIO2) and annual mean temperature (BIO1; Table S3). Thus, the negative values of PC1 are colder and drier conditions and positive values are warmer and wetter.

Phylogenetic regression between climatic variables and xylem anatomical traits showed that species' climate of origin is an important predictor of wood anatomy properties within the oak clade (Figure 2; Table S4). Specifically, PC1 was positively associated with vessel hydraulic diameter (D_{mh}), specific hydraulic conductivity (K_{theo}), conductivity index (I_{k}), size to number ratio (S), vessel area (VA) and negatively associated with the number of vasicentric tracheids (VT; Figure 2a–i; Figure S1). Among all the climatic variables, two—temperature of the driest quarter (BIO 9) and precipitation of the driest month (BIO 14)—were selected as the main explanatory variables by multiple phylogenetic regression analyses (Figure 2). Other important climatic variables explaining xylem trait variability include mean annual precipitation (BIO12) and mean annual temperature (BIO1). Species from more arid regions and with colder temperatures (PC1), and regions with a hot dry season and seasonal precipitation patterns had smaller D_{mh}, lower K_{theo}, higher VT, lower I_{k}, lower VA, lower S and higher VD (Figure 2a–f; Figure 3; Figure S1; Figure S2). The xylem traits that were not explained by the temperature of the driest quarter and precipitation of the driest month include vessel fraction (VF), pit diameter (Pit_{D}), pit membrane area (Pit_{A}) and pit fraction (Pit_{F}; Table S4). Many of the significant trait–climatic variable associations (Figure 2a–i) were not significant when only using individuals within a single garden (Figure 2j), that was also true when we analysed the data based on leaf phenology, probably due to the lower statistical power when using a smaller sample size. All sampled species presented vasicentric tracheids and increased

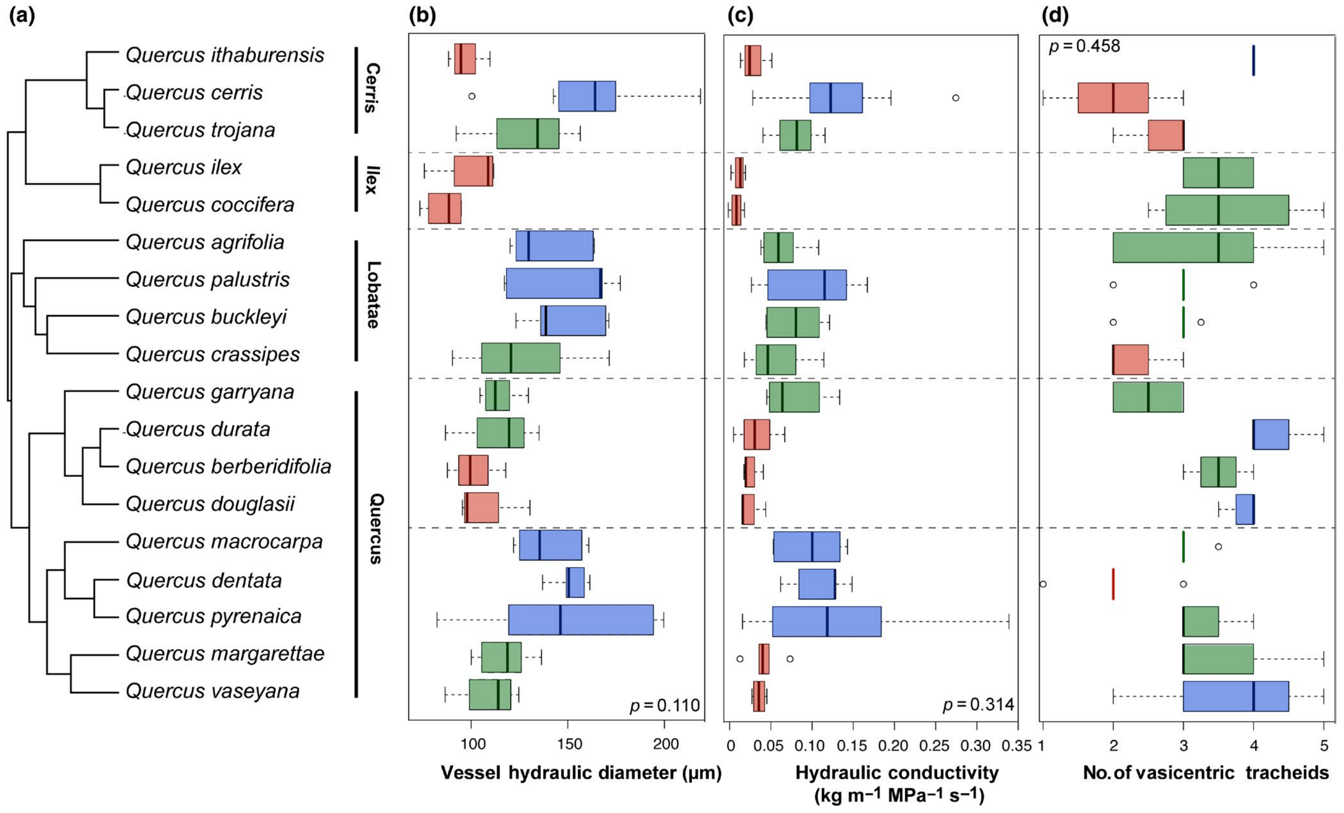

FIGURE 1 (a) Phylogenetic relationships of the 18 studied oak species based on single nucleotide polymorphism obtained by ddRAD sequencing extracted from Hipp et al. (2020). Labels to the right of the tree indicate sections (black line) following the accepted taxonomy for the genus (Denk et al., 2017). The mean and variance are shown with box and whisker plots for each species for mean vessel hydraulic diameter (μm; b), theoretical hydraulic conductivity (kg m^{-1} MPa^{-1} S^{-1}; c) and number of vasicentric tracheids (d). The blue, green and red colours indicate high, mid and low mean values, respectively, of vessel hydraulic diameter, theoretical hydraulic conductivity and number of vasicentric tracheids. The grey horizontal dashed lines separate the species in the different sections: *Cerris*, *Ilex*, *Lobatae* and *Quercus* (divided into Western oaks at the top and Eastern oaks at the bottom). The *p*-values indicate the significance of the ANOVA test among sections

VT presence was associated with highly seasonal environments that experienced low temperatures during cold months (negative PC1 values), a dry-hot time of year (high temperature in the driest quarter) and a seasonal period of low water availability (low precipitation in the driest month; Figure 2).

3.3 | Intraspecific variability of wood anatomical properties

Four anatomical traits (out of 11), VT, Pit_F, D_{mh} and VD had significant intraspecific trait variation across the CA and FR gardens (Figure 4a–d, Table S5). The number of vasicentric tracheids (VT) was ~25% higher at the more arid California climate than in France where annual precipitation is higher. Mean Pit_F was ~20% lower in California than in France. Mean D_{mh} and mean VD were ~15% lower and 34% higher, respectively, in California than in France indicating that these oak species tend to have smaller vessel size but higher vessel density in arid areas compared to humid environments. All the other seven traits, K_{theo}, I_k, VA, *S*, VF, Pit_D and Pit_A, did not significantly differ between individuals of the same species growing in different gardens (Figure 4e). Furthermore, we did not detect any significant intraspecific variation between any of the 11 traits measured when comparing CA and EN gardens (Table S5). Together, these results indicate limited plasticity of wood anatomical traits and suggest that plastic responses depend on the environmental gradient that the species are experiencing. Finally, leaf phenology had a significant effect on D_{mh}, I_k, VF, K_{theo} and Pit_F (Table S5), indicating that species with long-lived leaves (i.e. evergreens) may have different wood anatomical properties, which can be linked to plant performance in different environments. The number of individuals sampled for each species per garden and species mean, minimum, maximum, standard deviation and coefficient of variation values of the 11 traits are shown in Table S6.

3.4 | Climatic niche and plastic responses of wood anatomical traits

The interaction between climatic niche and the local growth environment—indicated by the garden the individuals were growing in—was the main source of variation for all the traits measured in this study (Figure 5). When considered separately, climate of origin explained most of the variation for 7 out of the 11 traits sampled

TABLE 2 Phylogenetic signal in species' wood anatomical traits calculated using Blomberg's *K* (Blomberg et al., 2003) for the 18 *Quercus* species collected in California-US, southwestern France and central England

Trait	*K*.obs	*K*.pval	*K*.sim_mean	*K*.sim_sd	*K*.sim_ses	*K*.BM_pval	*K*.BM_mean	*K*.BM_sd	*K*.BM_ses
D_{mh}	0.445	0.507	0.473	0.138	−0.199	**0.006**	1.015	0.302	−1.889
K_{theo}	0.353	0.817	0.480	0.147	−0.863	**0.001**	0.994	0.309	−2.073
VT	0.460	0.464	0.476	0.148	−0.111	**0.015**	1.010	0.323	−1.703
I_k	0.483	0.428	0.481	0.154	0.011	**0.015**	1.000	0.300	−1.723
VD	0.400	0.641	0.477	0.151	−0.507	**0.003**	1.004	0.322	−1.878
VA	0.562	0.218	0.480	0.144	0.569	**0.050**	1.000	0.296	−1.478
VF	0.480	0.497	0.491	0.147	−0.073	**0.017**	0.993	0.297	−1.724
S	0.425	0.588	0.477	0.146	−0.356	**0.005**	1.005	0.304	−1.908
Pit_D	0.474	0.418	0.478	0.148	−0.024	**0.006**	1.004	0.290	−1.828
Pit_A	0.231	0.988	0.490	0.158	−1.648	**0.001**	1.008	0.307	−2.530
Pit_F	0.357	0.774	0.483	0.166	−0.761	**0.003**	0.984	0.291	−2.153

Note: We report *K*.pval as the *p*-values based on a tip randomization test ($N = 1,000$) to determine if estimates significantly departed from expectations if there was no phylogenetic signal (species were randomized across the tips of the phylogeny); and *K*.BM.pval the probability of the observed value being smaller than the expected under a Brownian model of evolution (1,000 simulated datasets). Significant values ($p \le 0.05$) are given in boldface. *K*.obs = observed *K* values; *K*.sim.mean = mean null model *K* values; *K*.sim.sd = standard deviation null model *K* values; *K*.sim.ses = standardized effect size of *K* (observed *K* − mean null *K*)/SD null; *K*.BM.mean = mean Brownian Motion (BM) model *K* values; *K*.BM.sd = standard deviation BM model *K* values; *K*.BM.ses = standardized effect size of *K* (observed *K* − mean BM *K*)/SD BM. For trait abbreviation, please refer to Table 1.

(Figure 5). The only three traits that the growth environment explained more trait variation than species' climatic niche were Pit_A, Pit_D and Pit_F. The most variable trait was *S* (coefficient of variation = 49.5%) followed by K_{theo} (43.9%) and VD (35%). whereas the least variable traits were Pit_D (13.6%), D_{mh} (15.4%) and Pit_F (19.3%; Table S6).

4 | DISCUSSION

Our results reveal that climate of origin is a good predictor of xylem traits. Species from drier regions had traits that conferred higher resistance to drought compared with species from mesic regions. Also, wood properties of the oaks exhibited low plasticity but high trait lability across the phylogeny, indicating that trait evolvability may be an important mechanism allowing oak species persistence in the different environments. Finally, the interaction between the climate of origin and growth environment explained most of the variation in the xylem traits, indicating that the degree of plasticity in response to the growth environment depends on the climate of origin and may itself be adaptive.

4.1 | Wood anatomical properties in the oaks are evolutionary labile

We found no evidence for phylogenetic signal among the wood traits. All the xylem traits were not significantly different from the white noise null model (tips of the phylogeny were randomized) but were statistically different from the Brownian motion (BM) model of evolution (Table 2), indicating the ability of these traits to be evolutionary labile during speciation. Furthermore, we found a pattern of phylogenetic overdispersion—species within a community are less closely related than expected—where species from different lineages co-occur in the same communities and have similar trait values indicating convergent evolution in xylem traits that are important for habitat specialization (Cavender-Bares et al., 2004). As a result, species in different sections have overlapping niche distribution, whereas species within a section have little niche overlap (Cavender-Bares, 2019). Our results support the hypothesis that oak species went through sympatric parallel adaptive radiation and sister taxa have repeatedly moved into different habitats (Hipp et al., 2018). Yet, a distinct pattern could be found when only particular lineages are analysed. For example, Skelton et al. (2021) reported large differences in xylem vulnerability to cavitation between Mediterranean white oak clades while closely related species within each clade varied little. Thus, both evolutionary processes can be happening at the same time: there is trait lability and convergent evolution when species across the whole phylogeny are analysed, and there is also trait conservatism in smaller lineages that are found in particular habitats (Cavender-Bares et al., 2018).

4.2 | Climatic niches predict xylem characteristics across the oak phylogeny

Our study reveals that many xylem properties within the oaks show evidence for correlated evolution with species' climatic niche. In alignment with our expectations, species from seasonally hot, more arid and colder winter climates had xylem traits that are associated with higher resistance to drought, such as lower vessel size per number ratio (*S*), smaller vessel hydraulic diameter (D_{mh}), lower stem hydraulic

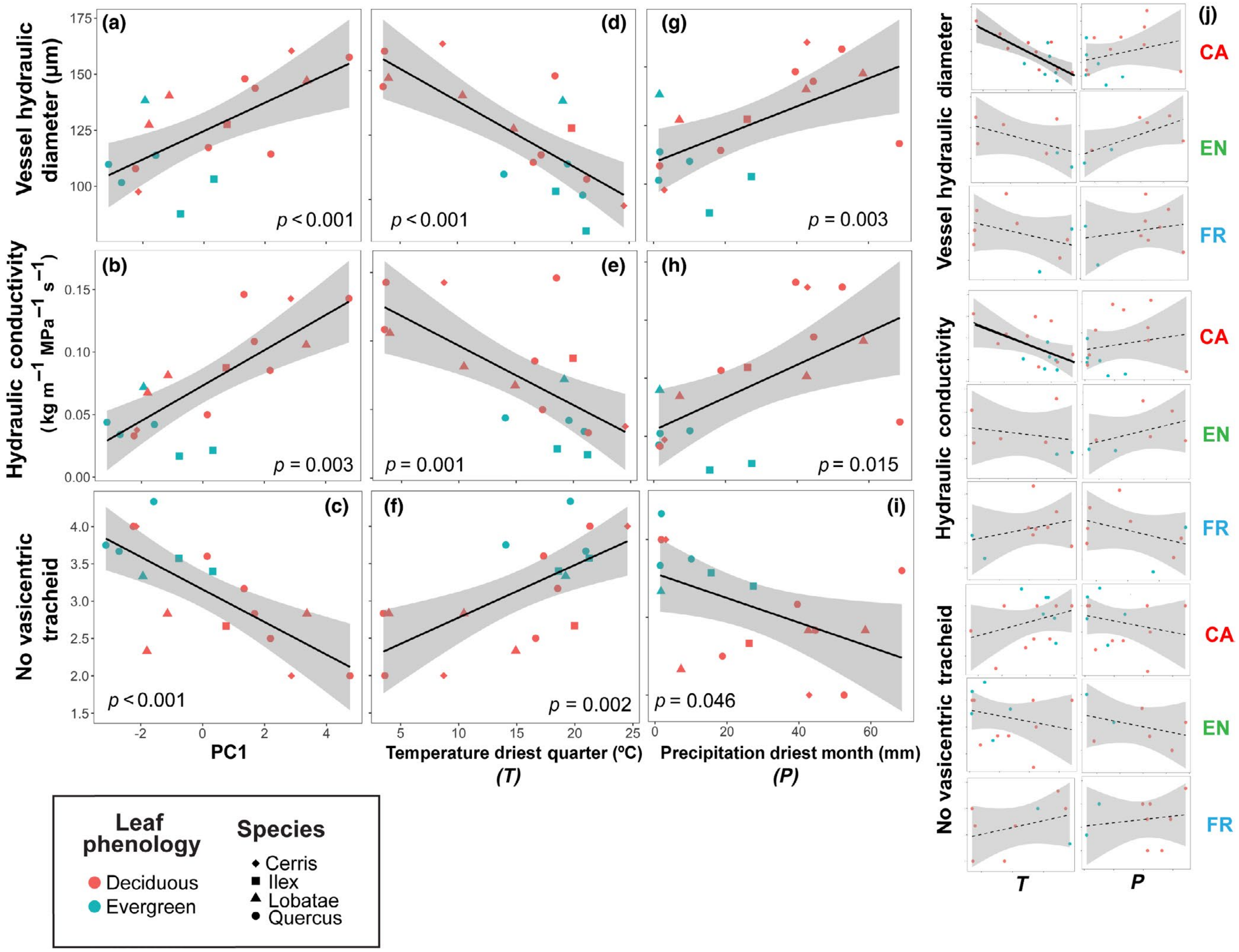

FIGURE 2 Phylogenetic relationships between the first principal components axis for climatic variables (PC1), the temperature of the driest quarter (T) and precipitation of the driest month (P), and (a, d, g) mean vessel hydraulic diameter, (b, e, h) theoretical hydraulic conductivity, and (c, f, i) number of vasicentric tracheids. Panels a–i indicate species' trait values normalized by overall species mean (individuals from all gardens are considered), while small panels (j) represent the phylogenetic relationship within each garden (CA = US-California, EN = England, FR = France). The different symbols represent the different sections following the study of Hipp et al. (2020). The solid lines indicate significant ($p \le 0.05$) and dashed lines indicate non-significant ($p \ge 0.05$) relationships and shaded areas are the confidence intervals

conductivity (K_{theo}), a higher number of vasicentric tracheids (VT), lower conductivity index (I_k), lower vessel area (VA, also referred to as vessel size) and higher vessel density (VD; Figure 1). For example, Mediterranean species, such as *Quercus coccifera* and *Q. ithaburensis*, experience a hot dry season and they presented smaller D_{mh}, lower K_{theo}, *S*, VA and VF than species from sub-Mediterranean regions with shorter dry seasons (e.g. *Q. cerris*) and temperate species such as *Q. dentata* and *Q. pyrenaica*, where mesic summers are usually observed. Interestingly, we did not find a significant evolutionary association between the pit traits measured in this study and species' climatic niches, suggesting that these traits may be less important for adaptation to local climates than other xylem attributes.

In addition to the precipitation and temperature variables assessed in this study, photoperiod sensitivity could also be influencing xylem properties within the oaks. However, only a small number of oak species are sensitive to photoperiod (Zohner et al., 2016), and the photoperiod sensitivity does not seem to be related with species' functional traits such as xylem anatomy (Way & Montgomery, 2015). Thus, evidence suggests that photosensitivity probably plays a relatively minor role in shaping wood growth patterns in the oaks.

The cellular structure of the xylem in plant stems has important implications for whole-plant function (Carlquist & Hoekman, 1985; Tyree & Ewers, 1991). For example, vessel size to number ratio (*S*) measures variation in the vessel composition within a transport space. Lower values of *S* indicate that the conducting area of the xylem is comprised of many small vessels (Zanne et al., 2010). These vessels with smaller D_{mh} should be less efficient in water transport (lower K_{theo}) but potentially at lower risk of embolism (Tyree & Sperry, 1989; Sperry et al., 2006; Jacobsen et al., 2019; but see Gleason et al., 2016). Our data indicate that oaks species from warmer and drier areas have smaller D_{mh} and K_{theo} (Figure 2), which may suggest a hydraulic safety efficiency trade-off. Furthermore, vessel diameter seems to be constrained by aridity,

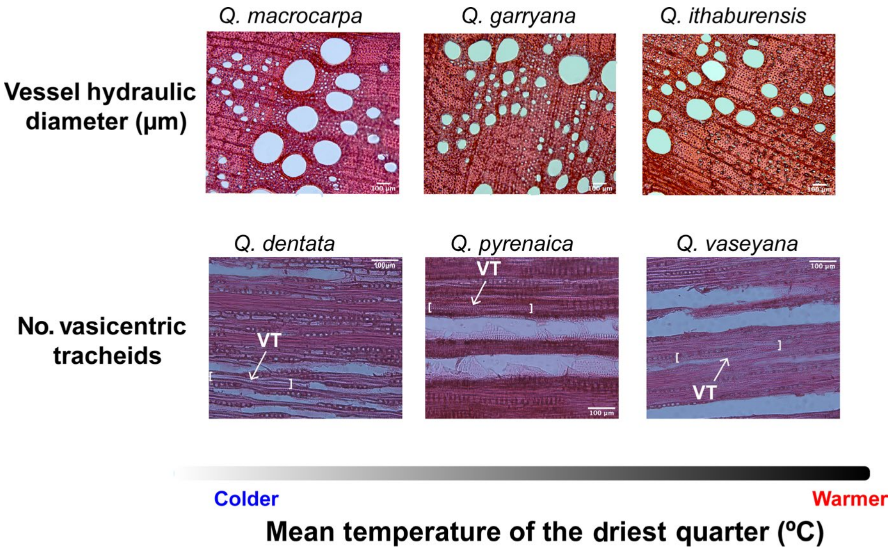

FIGURE 3 Cross-section images at the top show xylem vessel hydraulic diameters of oak species from different climates, as indicated by species mean temperature distributions (mean temperature of the driest quarter, °C). Shown are *Quercus macrocarpa* (mean 3.5°C), *Q. garryana* (mean 16.6°C), and *Q. ithaburensis* (mean 24.5°C). The images at the bottom are transversal sections displaying vasicentric tracheids in an area of 8000μm^2 for *Q. dentata* (mean 3.6°C), *Q. pyrenaica* (mean 18.5°C) and *Q. vaseyana* (mean 14°C). The white scale bars on the images are 100 μm. The relationship between vessel hydraulic diameter, number of vasicentric tracheids and mean temperature of the driest quarter is shown in Figure 2d and 2f, respectively

with a broader range of D_{mh} in more humid areas (Hacke et al., 2017). Also, narrow vessels are associated with a wide range of P_{50} in a variety of plant species including oaks, while wide vessels tend to be vulnerable (Hacke et al., 2017; Percolla et al., 2021). Together, these results support the key role of narrow vessel diameters and low density as drought tolerance traits in oaks, allowing plants to locally adapt to highly seasonal and drier regions.

Vasicentric tracheids (VT) were present in all the oak species sampled in this study and their presence was negatively correlated with aridity in the climate of origin, such that species from low humidity, seasonal (low minimum temperature and high dry season temperature), drier and hotter climates had higher numbers of VT than species from milder mesic regions. Vasicentric tracheids are very small conduits—both narrow and short—that are adjacent to and surrounding vessels. While they likely have limited contribution to water transport under well-water conditions when most vessels are functional (approximately 5%–15% of flow as reported in Percolla et al., 2021), these tiny conduits are hypothesized to provide alternative pathways when large vessels become embolized (Carlquist, 1985; Fontes & Cavender-Bares, 2020; Pan & Tyree, 2019; Pratt et al., 2015), and their functionality in sap transport can be directly observed using microCT (Pratt & Jacobsen, 2018). Yet, we ignore how prevalent they are, and they are likely more frequently found in particular plant groups, like oaks, than in others (Fontes & Cavender-Bares, 2020). Our results suggest that VT are important to drought tolerance and their presence is expected to have a negative relationship with xylem vulnerability to embolism (Pratt et al., 2015). Despite being present in more than a third of the species present in dry habitats (Carlquist & Hoekman, 1985) and their clear importance for water regulation, VT remain largely understudied. When xylem vessels embolize, they become water reservoirs that can be redirected to VT maintaining the flow of water through unfavourable seasons. Given our results and the prevalence of VT in dry habitat species, the evolution of this trait may have allowed oaks to by-pass the safety efficiency trade-off—imposed by their large vessels—and radiate to environments that would have otherwise been too dry or cold for them to thrive.

Oaks from mesic regions tend to have higher K_{theo}, D_{mh}, S, VA and I_k than species from arid regions, suggesting a greater potential to transport water more efficiently. Species from mesic environments tend to show an acquisitive resource-use strategy hypothesized to increase competitive abilities that can be beneficial where resources are abundant (Reich, 2014). For example, plants with a greater maximum hydraulic conductivity support faster growth and may be stronger competitors in high precipitation environments, whereas trees that have low hydraulic conductivity may be selected against or outcompeted from these humid habitats (Chapin, 1991; Reich, 2014). We acknowledge that the traits measured in this study may not represent all of the most important traits underlying habitat partitioning in the oaks (e.g. Fallon & Cavender-Bares, 2018; Furze et al., 2021; Ramírez-Valiente et al., 2020; Skelton et al., 2019), yet our results indicate that xylem anatomy shows correlated evolution with climate in oaks and that evolutionary shifts in hydraulic architecture are an important mechanism by which species have adapted to local precipitation and temperature regimes.

4.3 | Most xylem traits show limited capacity to respond to varying climates

We found little evidence for intraspecific variation in xylem anatomical traits among species growing in the Unites States-CA, England and France (Figure 4), consistent with other studies (Granda

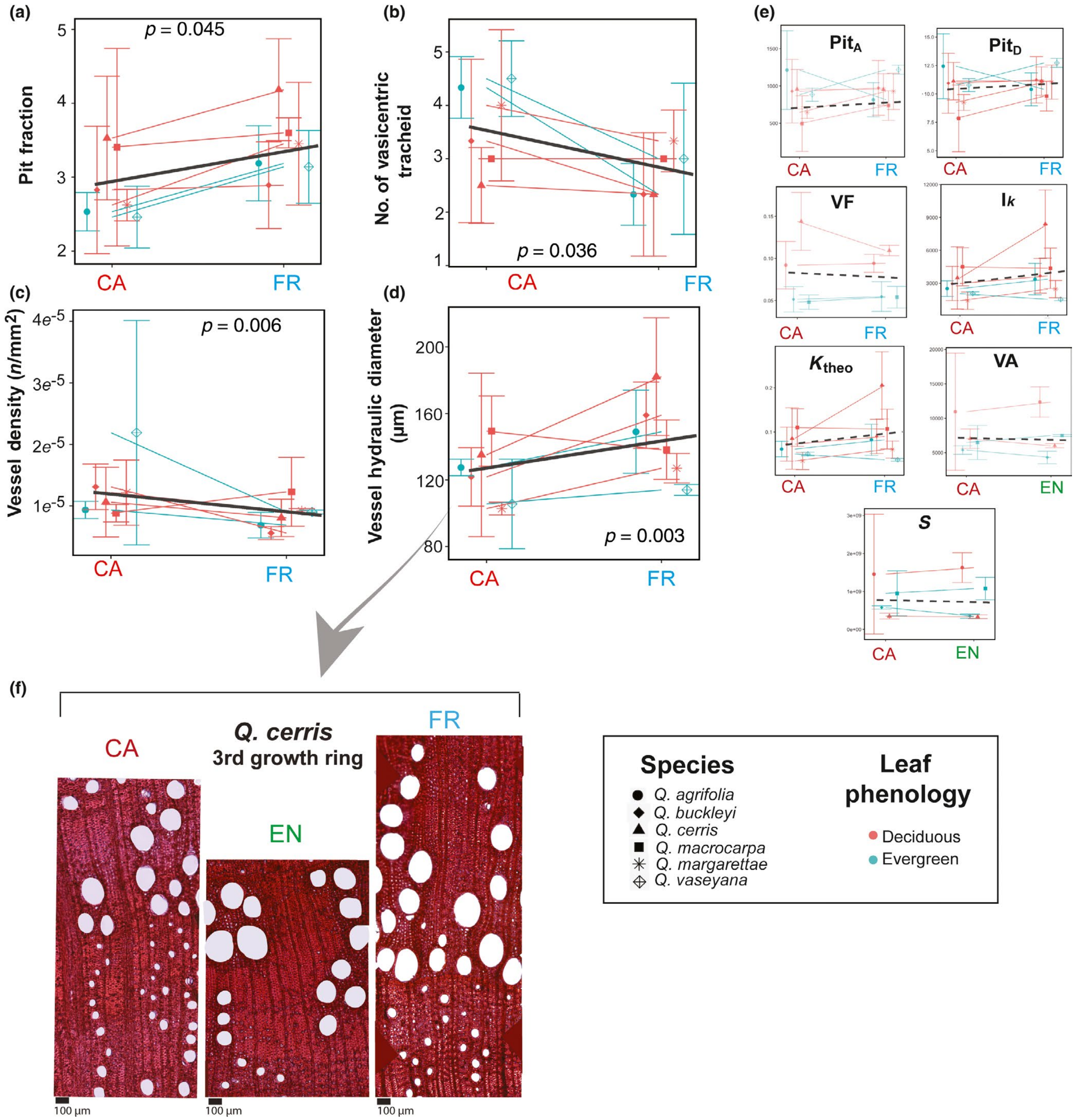

FIGURE 4 The intraspecific variation of (a) pit fraction, (b) the number of vasicentric tracheids, (c) mean vessel density and (d) mean vessel hydraulic diameter for nine species of *Quercus* (different symbols) sampled in three different gardens, US-California (CA), England (EN) and France (FR). Panels a–d represent the only instances where traits showed significant plasticity across gardens ($p \leq 0.05$; solid grey line) and small panels (e) display selected traits that showed non-significant ($p > 0.05$; dashed grey line) intraspecific trait variation among the gardens. Pit_A = mean pit membrane area; Pit_D = mean pit diameter; VF = mean vessel fraction; I_k = conductivity index; K_{theo} = theoretical hydraulic conductivity; VA = mean vessel area; S = vessel size to number ratio. The dots are species' mean trait values within each garden and bars are standard errors. The images at the bottom (f) correspond to the cross-section of the third growth ring of the ring porous species *Quercus cerris* growing in US-California (CA), England (EN) and France (FR). The black bars represent 100 µm

et al., 2018; Percolla et al., 2021; Skelton et al., 2019). The only four traits that were significantly different among the three locations were pit fraction (Pit_F), number of vasicentric tracheids (VT), mean vessel density (VD) and mean vessel hydraulic diameter (D_{mh}). While leaf traits in the oaks may exhibit a high ability to acclimate to a drier environment (e.g. Cavender-Bares & Ramírez-Valiente, 2017; Ramírez-Valiente et al., 2010), many xylem properties do not seem very plastic and may be better explained by species adaptation to

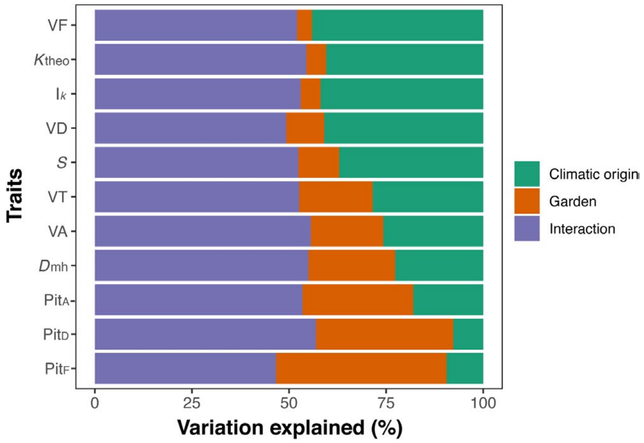

FIGURE 5 Variance decomposition (bar colours) of 11 traits across climatic variables from the source population, gardens (local environment) and their interaction. D_{mh} = mean vessel hydraulic diameter; K_{theo} = theoretical hydraulic conductivity; I_k = conductivity index; VT = number of vasicentric tracheid; VF = mean vessel fraction; VA = mean vessel area; VD = mean vessel density; S = mean vessel size per number ratio; Pit_A = mean pit membrane area; Pit_D = mean pit diameter; Pit_F = mean pit fraction

its climate of origin. Low trait plasticity and a high level of local adaptation can reduce important genetic variation due to species specialization to a particular environment (Gharehaghaji et al., 2017). Introgression is important for adaptation in the oaks (Valencia-Cuevas et al., 2014) and has been shown to play a central role in successional processes by allowing species to colonize new habitats (Lexer et al., 2004). Thus, considering the limited plasticity in wood traits within the oaks, other mechanisms such as high trait lability (see next section) and introgression may be critical for maintaining trait diversity, allowing oak species to radiate and persist across different climatic regions.

Pore size and the fraction of inter-vessel pit membranes have a large effect on the hydraulic conductivity (efficiency) of the xylem and its vulnerability to embolism (safety; Wheeler et al., 2005). Larger pit membrane areas may increase the likelihood of large pore presence, permitting embolism to spread through the xylem at lower tensions (Christman et al., 2009, 2012). The influence of pit structure on hydraulic resistance and vulnerability to drought (Jacobsen et al., 2016; Lens et al., 2011) suggests that it is an important adaptive trait with the potential to drive ecological differences between species. We show that pit traits were not associated with species' climatic niche but Pit_F was significantly different among the gardens, with higher values in more humid areas such as France (Figure 5a). A large Pit_F would increase the probability to have disproportionately large pit membrane pores leading to embolism spread and higher vulnerability to drought, in agreement with the rare pit hypothesis. The rare pit hypothesis (also called 'pit area hypothesis') states that the vulnerability of a given vessel is influenced by the inter-vessel pit area it contains, so vessels with greater pitted area have a greater chance of having more vulnerable pit (Venturas et al., 2017). Assuming a constant pit area per vessel area fraction, wider vessels will have greater cumulative inter-vessel pit area than narrow conduits (Christman et al., 2012; Hacke et al., 2017; Wheeler et al., 2005). Our results strengthen the importance of pit properties as a drought resistance structure that can help plants survive in drier regions. Also, pit traits, unlike VD, D_{mh} and VT that were significantly associated with both climate of origin and local environment, do not seem to be as adapted to the climate of origin as other xylem traits but may play a key role in helping plants acclimate to different environmental conditions.

4.4 | Climate of origin and plastic capacity interact to determine wood traits across the oaks

Maintaining high genetic diversity and plastic capacity are ways in which plants can persist in fluctuating climates, particularly when generation times are long, and an individual plant may experience a range of environments throughout the course of its life span (Cavender-Bares & Ramírez-Valiente, 2017; Sáenz-Romero et al., 2017). Selection due to climate and plastic responses to local growth environment drive species' range limits and disentangling their separate influence may help understand how plants will respond to climate change. We found that climatic niche was more important in explaining variability in xylem traits than local environment (Figure 5), indicating adaptive divergence in xylem properties among species with contrasting climates of origin. Interestingly, pit traits (Pit_A, Pit_F and Pit_D) were the only ones in which environmental conditions explained more trait variability than local climate, fortifying the key role that pit characteristics may play in helping plants adjust to variable habitats. However, these results should be taken with caution since we did not account the source population of the individuals sampled in this study (data not available), and differences among the locations may be due to genetic differentiation of source populations, limiting our ability to separate plasticity from evolutionary responses.

5 | CONCLUSIONS

From a wood anatomical perspective, oaks tend to have small vessels for a given vessel density, relative to other angiosperms, resulting in a lower lumen fraction, which affects xylem hydraulic conductivity. Also, we show for the first time that the number of vasicentric tracheids is negatively associated with aridity, low temperatures (see also Percolla et al., 2021) and temperature during the driest part of the year. The presence of VT is a relatively poorly explored xylem trait that may have key role for water regulation in the oaks, allowing plants to survive under drought conditions. Since it was first proposed as a drought survival mechanism (Carlquist, 1985), we have little advanced on the importance and function of vasicentric tracheids (however, see Percolla et al., 2021; Pratt et al., 2015). From an evolutionary perspective, wood traits of oak species are adapted to climate of origin and show limited plasticity. Yet, xylem traits within the oaks are flexible in terms of their ability to evolve and this flexibility in trait evolvability, together with interspecific gene flow, may be critical in the long-term persistence of the oaks across varying environments. Finally, studies, such as ours, that investigate species adaptation to distinct climatic regimes and identify the functional traits that underline these adaptations, as well as the mechanism that allows species persistence in different environments, are important for understanding ecosystem responses to climate change.

ACKNOWLEDGEMENTS

We thank Béatrice Chasse, Gérard Lionet, David Coomes, Cathleen Lapadat and Celine Bares for assistance with wood sample collection and preparation. We thank the Pouyouleix Arboretum in France, the Sir Harold Hillier in England and the Peter J. Shields Oak Grove at UC Davis arboretum in California for access to the materials and logistical support. We thank Gerard Sapes and Béatrice Chasse for valuable comments and edits on the manuscript. Permit PCIP-19-00256 from the US Department of Agriculture was used for importation of samples to the U.S.NSF DBI 2021898 and NSF DEB 1146380. The authors have no conflict of interest to declare.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

C.G.F. and J.C.-B. planned and designed the research and conducted the fieldwork; C.G.F., J.C.-B., A.L.J. and R.B.P. designed the laboratory protocols; C.G.F. and J.P.-L. performed the statistical analyses; C.G.F. performed the measurements and wrote the manuscript; C.G.F., J.C.-B., A.L.J., R.B.P. and J.P.-L. revised and provided comments on the manuscript; J.C.-B. provided financial and logistical support.

DATA AVAILABILITY STATEMENT

Data are accessible from Dryad Digital Repository, https://doi.org/10.5061/dryad.5hqbzkh74 (Fontes et al., 2021).

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How to cite this article: Fontes, C. G., Pinto-Ledezma, J., Jacobsen, A. L., Pratt, R. B., & Cavender-Bares, J. (2022). Adaptive variation among oaks in wood anatomical properties is shaped by climate of origin and shows limited plasticity across environments. *Functional Ecology*, 36, 326–340. https://doi.org/10.1111/1365-2435.13964