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Multi-variable approach pinpoints origin of oak wood with higher precision

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Abstract

Aim: Spatial variations of environmental conditions translate into biogeographical patterns of tree growth. This fact is used to identify the origin of timber by means of dendroprovenancing. Yet, dendroprovenancing attempts are commonly only based on ring-width measurements, and largely neglect additional tree–ring variables. We explore the potential of using wood anatomy as a dendroprovenancing tool, and investigate whether it increases the precision of identifying the origin of oak wood. Since different tree–ring variables hold different information on environmental conditions prevailing at specific times of the growing season—which vary between source regions—we hypothesize that their inclusion allows more precise dendroprovenancing.

Location: Europe, Spain.

Taxon: *Quercus robur* L., *Quercus petraea* (Matt.) Liebl., *Quercus faginea* Lam., *Quercus pyrenaica* Willd.

Methods: We sampled four oak species across Northern Spain, i.e. from the Basque country and Cantabria and—in the Basque country—from low to high elevation (topographic/latitudinal gradient). We measured multiple tree–ring variables to (a) extract complementary variables; (b) present statistical relations among them; (c) analyse region-specific variation in their patterns based on time–series of individual trees; and (d) determine underlying climate–growth relationships. Leave-one-out analysis was used to test whether a combination of selected variables allowed dendroprovenancing of a randomly selected tree within the area.

Results: A combination of latewood width (LW) and earlywood vessel size was used to pinpoint the origin of oak wood with higher precision than ring width or LW only. Variation in LW pinpointed the wood to east and west areas, whereas variation in vessels assigned wood to locations along a latitudinal/topographic gradient. The climatic triggers behind these gradients are respectively an east–west gradient in June–July temperature and a north–south gradient in winter/spring temperatures. The leave-one-out analyses supported the robustness of these results.

Main conclusions: Integration of multiple wood–xylem anatomical variables analysed with multivariate techniques leads to higher precision in the dendroprovenancing of ring-porous oak species.

1 | INTRODUCTION

Trees are affected by a set of spatially and/or temporally varying environmental factors, such as precipitation, temperature, competition, soil type, and many others. The combined effect of these local environmental factors on tree growth is reflected in the width and structure of the tree rings, and can be used to characterize a given species growing under specific site conditions (Babst et al., 2013; Holz, Hart, Williamson, Veblen, & Aravena, 2018; Martin-Benito & Pederson, 2015; Vicente-Serrano, Camarero, & Azorin-Molina, 2014). In dry Mediterranean areas, where trees have limited access to ground water, drought-induced water shortage was observed as the main growth-limiting factor (de Luis et al., 2011; Martin-Benito, Beeckman, & Cañellas, 2013; Olano et al., 2014). Under increased vapour–pressure deficit trees transpire more, which leads to a faster depletion of plant-available soil moisture. A decreasing soil–water potential initiates stomatal closure in the leaves to prevent drought-induced mortality (McDowell et al., 2008). The associated reduction of photosynthesis limits tree growth and leads to the formation of narrow tree rings (Bréda, Huc, Granier, & Dreyer, 2006). In contrast, at higher latitudes and elevations, temperature has been found as the main factor limiting tree growth (Grudd, 2008; Körner & Paulsen, 2004; McCarroll et al., 2013; Yang, He, Melvin, Zhao, & Briffa, 2013). Low temperatures limit the trees' photosynthetic rate, which leads to reduced growth rates (Petit, Anfodillo, Carraro, Grani, & Carrer, 2011). Trees growing under moderate conditions, e.g. in Central European lowlands or in Atlantic regions, exhibit more complex relationships between environment and growth with often multiple growth-limiting factors (Gričar, de Luis, Hafner, & Levanič, 2013; Souto-Herrero, Rozas, & García-González, 2018a) but their growth patterns are still indicative for the specific environment–growth interactions at a given site through time.

Environmental information on growing conditions as stored in tree rings is widely used to predict growth responses of trees to climate change (Holz et al., 2018; Williams, Michaelsen, Leavitt, & Still, 2010), to model potential future species distribution (Gutiérrez, Snell, & Bugmann, 2016; van der Maaten et al., 2017), to quantify forest resistance to drought events (Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017) and to reconstruct growth-limiting climate factors during the pre-instrumental period (Čufar, De Luis, Zupančič, & Eckstein, 2008; Rydval et al., 2017; Schofield, Barker, Gelman, Cook, & Briffa, 2016). Information on spatial variation of climatic signals in tree rings is also important for archaeological and historical studies, as it serves as a basis for dating and determining the geographical

origin of historical timbers ("dendroprovenancing") (Speer, 2010). This can be used to identify source areas of wood, as well as for reconstructing wood–trade networks (Domínguez-Delmás et al., 2015). Nowadays, dendroprovenancing is becoming more and more important also in terms of detection of illegal logging (Kagawa & Leavitt, 2010; Vlam et al., 2018). Moreover, ancient timber contains information about past forest-management practices (Haneca, Boeren, Van Acker, & Beeckman, 2006), and reflects technological choices, such as selection of species for particular elements of ships or buildings, and also types of tools used for wood processing (Billamboz, 2003; Castro, 2008; Tegel, Elburg, Hakelberg, Stäuble, & Büntgen, 2012). Dendroprovenancing was successfully applied to identify the origin of foundation piles under historical buildings in the Netherlands (Sass-Klaassen, Vernimmen, & Baittinger, 2008) or wood from shipwrecks (Bridge, 2011; Domínguez-Delmás, Nayling, Ważny, Loureiro, & Lavier, 2013), and to unravel the Baltic wood trade (Ważny, 2002). Dendroprovenancing of wood from shipwrecks is considered as the most challenging, since boats and ships may be found far away from the construction place (Bridge, 2012), which is not necessarily related to the timber source areas and, single shipwrecks may contain wood from different origins (Haneca, Čufar, & Beeckman, 2009).

Until now, dendroprovenancing is almost exclusively based on correlation analyses between ring-width series and a set of reference ring-width chronologies. A statistically significant match leads to dating and provenancing of a given ring-width sequence (indicated by the area covered by the reference chronology) (Fowler & Bridge, 2017). In some specific areas, stable isotopic ratios have also shown great potential to be used in provenancing studies (Bridge, 2012). In combination with dendrochronological methods, carbon, oxygen and sulphur isotopes have been used to improve the spatial resolution of provenancing (e.g. Kagawa and Leavitt 2010; Horacek 2012), discriminate between species (Horacek, Jakusch, & Krehan, 2009), and to identify wood origin (Gori, Wehrens, La Porta, & Camin, 2015). Strontium stable isotopes have also demonstrated good potential for provenancing cedar ship timber (Rich et al., 2016). However, the isotopic composition of wood can be influenced by biological and physicochemical processes not related to geographical/climatic factors (Hajj, Poszwa, Bouchez, & Guerold, 2017) and for archaeological wood further care is needed as processes such as diagenesis in soils can modify wood composition (Hajj et al., 2017). Extending dendroprovenancing with techniques that use geographically and climatically bound proxies has the potential to strongly improve its accuracy.

Recently, the potential of using additional wood-anatomical variables besides ring width has also been investigated. Esteban, Martin, de Palacios, and Fernandez (2012) found that variation of wood biometry of a pine species was higher and more pronounced among provenances than within populations. A first attempt to include annual changes in maximum latewood density of a tree ring showed that the probability of successfully dating historical samples can be greatly increased (Wilson et al., 2017). The recent development of new techniques (Gärtner & Nievergelt, 2010), and improvements in image analyses (von Arx & Carrer, 2014) opened new perspectives for using more quantitative wood-anatomical variables for dendro-provenancing studies (Haneca et al., 2009).

In this study, we explored and tested the possibility to use a multi-variable approach on ring-porous oak, a species group that is widely used in historic constructions. In the context of the multidisciplinary project ForSEAdiscovery (htttp://forseadiscovery.eu), we investigated whether using oak earlywood (EW) vessel properties and latewood width (LW) can improve the precision of ring width based dendroprovenancing and, if so, what anatomical variables drive the improvement in such a multi-variable approach. We hypothesize that integrating EW vessels and LW leads to a more precise determination of the source area of a given oak timber, because both variables contain different and complementary climate signals which designate the wood to specific areas where combinations of these climate signals prevail.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

Samples were collected from nine oak forest stands in the Basque Country (six sites) and Cantabria (three sites) in Northern Spain (Figure 1).

These forests were selected because they served as wood-source areas for shipbuilding in the 16th to 18th centuries (Martínez Ruiz, 1999). We sampled trees in the Basque country (eastern sites) and in Cantabria province (western sites) (Figure 1) with an elevational gradient in the Basque country (from 80 to 1,181 m a.s.l.). The eastern sites (AZK, UZK, OIR, GOR/GOY, OTE and SVA) are located along a phytogeographical gradient (Table 1), with a gradual change of vegetation from Euro–Siberian in the North to more Mediterranean towards the South, and a gradient in elevation ranging from 80 m a.s.l close to the coast to 954 m a.s.l. further inland (Table 1). The northeastern sites (AZK, UZK and OIR) have typical Euro–Siberian vegetation dominated by *Quercus robur*. AZK and UZK were intensively used for charcoal production in the past but are not managed nowadays. OIR is a private-owned forest patch in the village of Oiartzun, with trees scarcely distributed on pasture land. The central eastern site (GOR/GOY) is located in the transitional zone between Euro–Siberian and Mediterranean vegetation and *Quercus pyrenaica* is the dominant tree species with some inclusions of *Q. petraea*. This site was heavily managed (coppiced) until the mid-20th century but was not managed since. Whereas the southeastern sites OTE and SVA consist of Mediterranean forests dominated by *Q. faginea*, with OTE

on steep hills and were not used/managed in the past, SVA mostly consists of old trees in flat pastureland (called *dehesa* in Spanish). All western sites (BRR/BRY, ONQ and ORT; Figure 1) feature typical transitional vegetation between Atlantic and Mediterranean phytogeographical regions, with the dominance of *Q. pyrenaica* in ORT and *Q. petraea* in ONQ. These sites share a similar mild climate, without a pronounced summer drought, and an altitudinal range from 1,037 to 1,181 m a.s.l. In our analyses we separate eastern from western sites (as categorical variables), and further separate eastern sites in northern, central and southern categories (NE, CE and SE respectively).

Selected oak species vary in their habitat and ecology and hence show specific distributional patterns. *Quercus robur* and *Q. petraea* are widely distributed in Europe whereas *Q. faginea* and *Q. pyrenaica* are largely restricted to the Iberian Peninsula (Table 2).

2.2 | Acquisition of ring-width and vessel-size time series

Sampling was performed in May/October 2015 and in October 2016. Between seven and 25 trees were sampled per site (Table 1). The variation of sample size per study site was caused by the different number of suitable trees at each site. Although oak species are prone to hybridize and many taxa were described for the Iberian Peninsula (Amaral Franco, 1990), we are confident of our species identification as we carefully identified each tree sampled at stands with coexisting oak species. The largest and apparently oldest oak trees with no visible damage to crowns or stems were selected and two to four 5-mm cores were extracted from each tree.

Samples were air dried, glued onto wooden holders, cut using a sliding microtome (Gärtner & Nievergelt, 2010), and sanded with progressively finer sandpaper (grain sizes from P180 to P1200, FEPA Abrasives). Tyloses (parenchyma outgrowths into vessels) and wood dust were removed using a high-pressure water blast, after which each core was stained using black ink. Chalk was rubbed on the samples to fill EW vessels, thus achieving better contrast of the vessels for image analyses.

Total ring width (TRW), EW and LW were measured using a Velmex measuring table (Velmex TA Unislide; Velmex Inc., Bloomfield, NY) coupled with a stereo-microscope (Olympus SZ60). Crossdating was done in two steps: first visually and then statistically. Visual crossdating was done by first matching the ring-width patterns of individual trees, and then different trees from the same site. Statistical crossdating was done using COFECHA 6.02P (Grissino-Mayer, 2001). Crossdating is considered as the most important principle of dendrochronology (Fritts, 1976), as it allows linking each tree ring to the exact calendar year of its formation.

For measurement of the EW vessel area, a sequence of overlapping images with a resolution of 13,780 dpi was taken from the wood surface using a digital camera (Canon EOS 600D) coupled to the stereo-microscope (Figure 2). The images were stitched using PTGUI 9.2.0 (New House Internet Services B.V., Rotterdam, The Netherlands). We measured vessels on a subset of trees and cores showing the highest inter-correlation (Table 1) as vessel measurements are labour intensive, and thus can be conducted on a limited
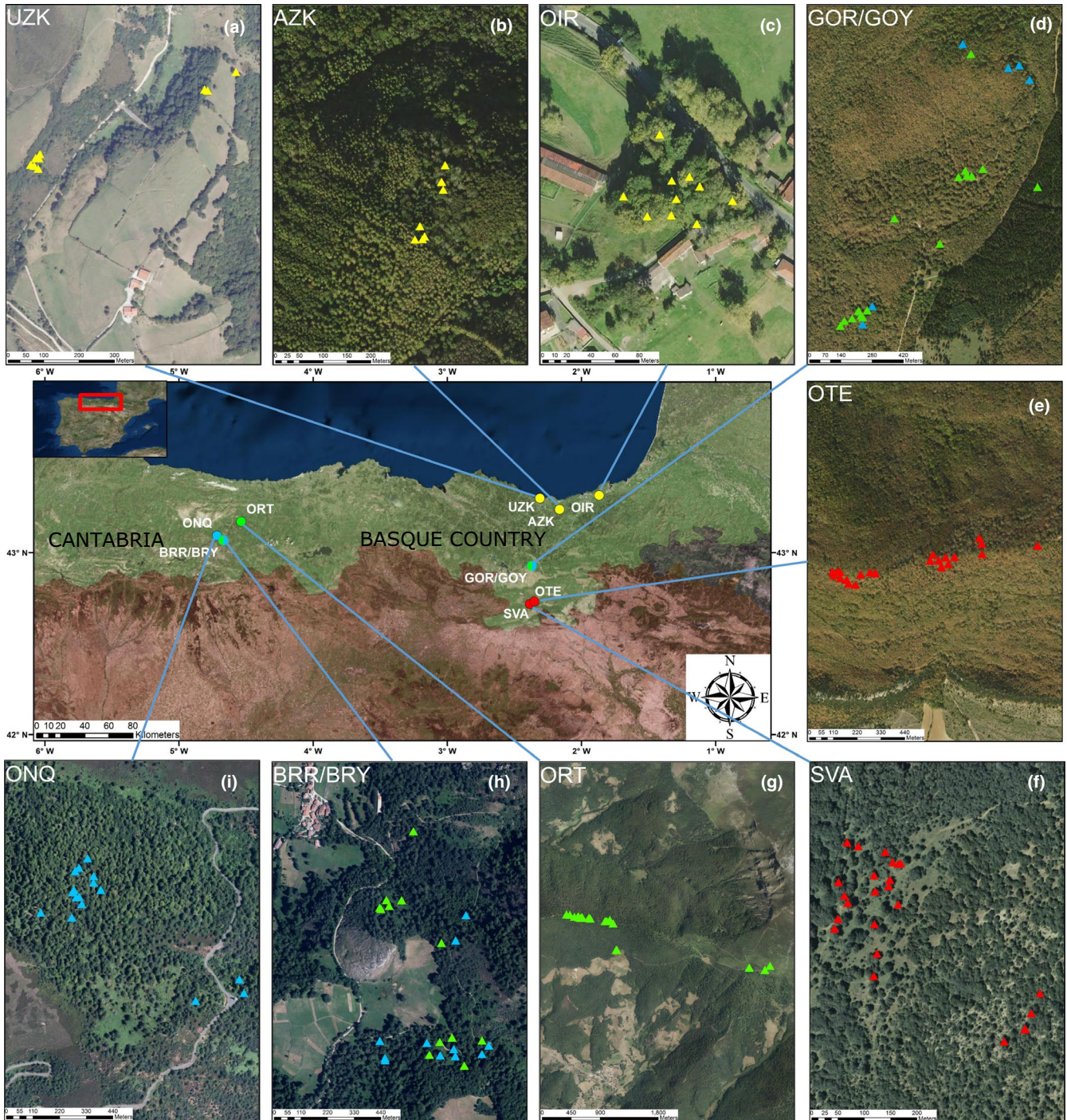
FIGURE 1 Location of study sites and distribution of sampled trees at each site (a–i). Dots represent selected forest stands (see Table 1 for an explanation of the abbreviations of site names), triangles represent selected tree individuals, *Quercus robur*—in yellow, *Quercus pyrenaica*—in blue, *Quercus petraea*—in green and *Quercus faginea*—in red, respectively. Sites with double names indicate the collection of two different species from the same forest stand. Transparent red, transparent green and transparent purple refer to the Mediterranean, Atlantic and Alpine biogeographical regions, respectively (https://www.eea.europa.eu/). Layer Credits: Source: Esri

number of trees only. Moreover, some cores were broken or had cracks, which made them less suitable for wood-anatomical analyses.

Earlywood vessels were measured semi-automatically in IMAGEJ 1.8.0 (Schneider, Rasband, & Eliceiri, 2012) using the VesselJ plugin (I. García-González, unpubl. data) and following the steps described in Souto-Herrero et al. (2018a). This plugin allows for efficient

discrimination of the bright chalk-filled vessel-lumen area from the dark-stained background (the remaining wood structures). After scanning and stitching, images were converted to 8-bit black-and-white and vessels were distinguished from the background using gray-scale thresholds. To ensure that undesired objects were excluded, additional filters were applied removing elliptical objects (less

TABLE 1 Overview on study-site characteristics and sampling design

Forest	Code	Coord.	Phyto-geographic region	Samp. region	Bed rock	Tavg (°C)	Prec (mm)	Elevation (m a.s.l.)	Species	TreesTR	TreesVESS
Azkorte	AZK	43°14' N 2°09' W	E	NE	SL	12	1,101	523	Quercus robur	7	6
Oiartzun	OIR	43°18' N 1°51' W	E	NE	SS	11.8	1,189	115	Q. robur	10	9
Uzkanga	UZK	43°17' N 2°18' W	E	NE	SL	12.8	1,199	80	Q. robur	9	9
Gordoa	GOR	42°55' N 2°22' W	T	CE	SS	9.7	878	1,129	Q. petraea	6	6
Gordoa	GOY	42°55' N 2°22' W	T	CE	SS	9.7	878	1,129	Q. pyrenaica	16	7
Oteo	OTE	42°43' N 2°23' W	M	SE	SL	10.4	653	829	Q. faginea	24	6
San Vicente de Arana	SVA	42°43' N 2°21' W	M	SE	SL	10.4	653	954	Q. faginea	25	7
Barrio	BRR	43°04'1 N 4°39'' W	T	W	SS	11.2	963	1,037	Q. petraea	11	10
Barrio	BRY	43°04' N 4°39' W	T	W	SS	11.2	963	1,037	Q. pyrenaica	12	9
On Quemada	ONQ	43°05' N 4°42' W	T	W	SS	11.2	963	1,118	Q. petraea	16	10
Orticeo	ORT	43°10' N 4°32' W	T	W	SS	11.2	963	1,181	Q. pyrenaica	18	10

Note. Bedrock: SS, sedimentary silicate; SL, sedimentary limestone; Coord., coordinates of the study site; Phytogeographical regions: E, Euro–Siberian; M, Mediterranean; T, the transition from E to M; Samp. region—sampling region: NE, CE, SE and W, northeastern, central eastern, southeastern and western sampling regions; Tavg, yearly average temperature (°C) of the corresponding study site; Prec, annual precipitation of the corresponding study site (mm), (climate data taken from CRU TS 4.01 (Harris et al., 2014)); TreesTR, number of trees used for ring width, earlywood width and latewood width measurements; TreesVESS, number of trees used for earlywood vessel measurements.

than twice as long as wide) and objects smaller than 10,000 μm². This particular size threshold was taken from Fonti and García-González (2004) and Fonti, Solomonoff, and García-González (2007) to exclude the smaller vessels formed later in the season, which may blur the climatic signal (García-González & Fonti, 2006), and also because most of the signal is recorded by the largest vessels, usually located in the first row (García-González, Souto-Herrero, & Campelo, 2016; González-González, Rozas, & García-González, 2014). The images with the detected vessels were then checked for detection errors and manual image corrections were performed where needed.

To assign each vessel to the corresponding dated tree ring, and to identify vessels belonging to the first-formed row at the beginning of the tree ring, we used the software package "Autovasos" (García-González, unpubl. data), again following Souto-Herrero et al. (2018a). From the EW-vessel measurements, 11 variables related to size, position, and water-conducting capacity were derived from each tree ring: hydraulically weighted vessel diameter (D_h), mean vessels area, maximum vessel size, number of vessels (NV), total vessels area, mean area of the first row vessels, hydraulic diameter (D_h) of vessels not belonging to the first row, mean area of vessels not belonging to the first row, maximum size of vessels not belonging to the first row, NV not belonging to the first row, and total area of vessels not belonging to the first row. D_h was calculated according to the equation:

$$D_h = \frac{\sum_{n=1}^{N} D_n^5}{\sum_{n=1}^{N} D_n^4}$$

where D_n (in μm) is the diameter of the vessel n (Sperry, Nichols, Sullivan, & Eastlack, 1994). D_h has been shown to be related to prevailing environmental conditions and to maximize the climatic signal (Pérez-de-Lis, Rossi, Vazquez-Ruiz, Rozas, & García-González, 2016; Souto-Herrero, Rozas, & García-González, 2017).

Before further processing, the individual time series of each variable were detrended to remove trends related to age and forest dynamics, using a cubic smoothing spline (Cook, Briffa, Shiyatov, & Mazepa, 1992) with a frequency response of 50% at a wavelength of 32 years. We subsequently used individual time series to compute site and regional chronologies. Site chronologies included only trees of each site × species combinations, while regional chronologies included trees from the predefined geographical regions, namely west, east as well as NE, CE and SE (in the east) regions of the study area (see Appendix S1 in Supporting Information for the detailed information on site TRW and D_h chronologies).

2.3 | Acquisition of a complementary set of variables

Many of the 14 measured or derived variables (3 ring width and 11 vessel-related variables) are correlated and carry redundant information (García-González et al., 2016). To reduce the number of variables to a subset of different, statistically meaningful variables, we used principal component analysis (varimax-rotated PCA) using the site chronologies calculated from the detrended individual time series. The selection was based on the ordination of variables according to the first two principal components (PCs). The resulting set of complementary variables, that contained different patterns of variation likely related to site-specific and climate-related signals, were included in subsequent analyses.

2.4 | Geographic patterns of time–series variability

Discrimination between patterns of annual variation in the selected variables was done based on the detrended individual time series of the trees from the nine study sites. Principal component gradient analyses (PCGA) (Buras et al., 2016) was performed in a time interval covered by most study trees (1888–2014). PCGA is based on loadings on the first two PCs obtained from an ordinary PCA, defining a gradient among time series based on their polar coordinates—in particular the angle—of the loadings (Buras et al., 2016). PCGA was used to test whether our predefined biogeographical gradients were reflected in the loadings which represent single trees on the first two PCs. To obtain statistical confidence in the observed patterns, we tested whether the polar angles representative of the loadings differed between source regions using Wilcoxon rank sum test. This individual tree approach, i.e. using time series of individual trees instead of site chronologies, was chosen since one of the aims was to investigate whether individual series of the selected variables

TABLE 2 Overview on study species characteristics, distribution and ecology

Species	Distribution	Elevation	Bedrock/Soil
Quercus robur	Europe (Eaton, Caudillo, Oliveira, & de Rigo, 2016)	0–1,300 m a.s.l. (Eaton et al., 2016)	Fertile, moist soils (Eaton et al., 2016)
Quercus petraea	Europe (Eaton et al., 2016)	0–2,000 m a.s.l (Eaton et al., 2016)	Fertile, moist soils (Eaton et al., 2016)
Quercus pyrenaica	Morocco, Iberian Peninsula and South-Western France (Nieto Quintano, Caudillo, & de Rigo, 2016)	0–2,100 m a.s.l. (Nieto Quintano et al., 2016)	Siliceous mountains, rarely limestone and dolomites (Nieto Quintano et al., 2016)
Quercus faginea (subsp. *faginea*)	Iberian Peninsula (Blanco Castro et al., 2005)	600–1,200 m a.s.l (Blanco Castro et al., 2005)	Basic soils (Jiménez Sancho, Díaz Fernández, Martín Albertos, & Gil Sánchez, 1998)

express site- and/or region-specific patterns. If so, this would indicate that their origin can be correctly identified. For application as a provenancing tool, this is especially relevant as often only time series of a single or a few trees are available for dendroprovenancing.

2.5 | Climate effect on PCGA gradient

The gradient obtained from the PCGA was further used to explore mechanisms possibly driving it. To do this, we focused on climate correlations of single tree-ring series, instead of calculating conventional climate-growth relationships based on site chronologies (Chen et al., 2015; Dorado-Liñán, Akhmetzyanov, & Menzel, 2017). We downloaded gridded CRU TS 4.01 temperature and precipitation data over the period 1901–2016 (Harris, Jones, Osborn, & Lister, 2014) from the KNMI climate explorer (https://climexp.knmi.nl/start.cgi) and correlated these climate data with each single ring-width and vessel series. To account for non-normally distributed data, we used Spearman's rank correlation in these analyses. Afterwards, we investigated whether these correlations varied significantly along the determined PCGA gradient using Spearman's rank correlation. In this analysis a strong correlation would indicate a directional variation of climate correlations along the PCGA gradient.

Moreover, to test the effect of the geographical origin on climate correlations, we also compared the individual climate correlations between the geographical categories using Wilcoxon rank sum test (for the comparison between east and west), as well as Kruskal–Wallis test (for the north, central and southeastern sites). Finally, we computed so-called regional chronologies, i.e. the average over all individual time series representative of each geographical category and performed the corresponding climate correlations. This was done to support the results from the single tree climate correlations.

2.6 | Species effect on PCGA gradient

In addition to testing the resemblance of geographical categories in the PCGA-loadings, we also explored whether the variation of PCGA-loadings was related to species. That is, we tested—in a similar manner as for the geographical categories—whether the PCGA-loadings differed between the species. This was done, on the one hand,

on all time–series per parameter (i.e. latewood width and vessels). On the other hand, we also did this analysis on the basis of data considering only those sites where two of the study species (Q. petraea and Q. pyrenaica) were co-existing (BRR/BRY and GOR/GOY).

2.7 | Identifying the area of origin

To test whether the origin of a randomly selected tree can be identified from PCGA, we performed a "leave-one-out" approach. For this, we successively selected each tree from the data set to test whether its origin could be correctly identified by means of PCGA. In order to do so, we excluded the respective tree from the data pool, and performed a PCGA on the remaining data set as explained in section 2.2. This analysis was done separately for LW and vessel time–series. Afterwards, we correlated the left-out time–series with the scores of the first two PCs of the corresponding PCGA and transformed these correlation values into PC-loadings. From these loadings we computed Euclidean distances to the loadings of all the other trees (those which were kept in the data for the PCGA) and computed the categorical mean Euclidean distances referring to geographical origins. If the mean Euclidean distance of the left-out tree to the other trees from the same geographical origin was lower in comparison to trees from a different geographical origin, we defined this as a correct assignment. As a measure of success of this approach, the percantage of correct assignments was calculated.

All calculations were done in R 3.4 (R Development Core Team, 2017) using the "dplR" (Bunn, 2010), "psych" (Revelle, 2017) and "treeclim" (Zang & Biondi, 2015) packages.

3 | RESULTS

3.1 | Selection of complementary variables

Based on the similarity of loadings on the first two PCs of Varimax rotated PCA, the number of variables for further analyses was reduced from 14 to three, i.e. NV, D_h, and LW, since they appeared to carry unique and complementary information for most of the study sites likely related to site-specific environmental signals (see Appendix S2).
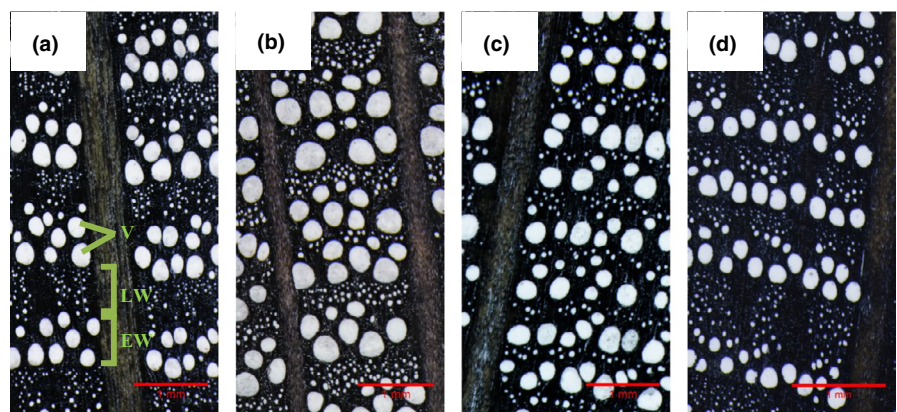
FIGURE 2 Wood surface images of: (a) *Quercus robur*, (b) *Quercus petraea*, (c) *Quercus pyrenaica* and (d) *Quercus faginea*. EW, LW and V indicate earlywood, latewood and vessels, respectively

3.2 | PCGA

The common overlap period for the PCGA of LW data was 127 years (1888–2014) and incorporated 64 individual trees representing all study sites and species. The PCGA demonstrated that LW time series were grouping according to geographical categories, i.e. there was a clear separation between the loadings representing trees of eastern and western origin (Figure 3) ($p < 0.01$, Wilcoxon test). Trees showed a similar grouping according to the loadings as derived from NV time series; however, there were more mismatches compared to LW (see Appendix S3).

D_h time series revealed no clear separation of loadings, neither across sites nor between the regions (see Appendix S4). Nevertheless, the application of PCGA only considering trees from the eastern sites, i.e. northeast—central east—southeast (NE—CE—SE), allowed grouping the trees according to the geographical categories based on D_h (Figure 4). In this analysis, the common overlap period used for the PCGA was 102 years (1913–2014) involving 35 trees. A Kruskal–Wallis test indicated significant differences of loadings between trees from NE, CE and SE ($p < 0.01$). At the same time, it was not possible to distinguish the CE trees from the other two sites on the basis of LW and NV (see Appendix S5).

3.3 | Climate effect on PCGA gradient

Correlation analyses between the gradient derived from the PCGA of LW time series and climate correlation scores indicate a strong effect for average June–July temperature on the PCGA gradient (see Appendix S6). Trees from the eastern sites were limited in LW formation by summer temperatures, whereas those from the western sites did not show any significant relationship between LW and early summer temperature (Figures 5a,b).

The strength of the climate correlations also varied along the PCGA gradient as derived from D_h (see Appendix S7). Vessel size (D_h) of trees in NE, located at lower elevation and closer to the sea was negatively correlated with February temperature, whereas for CE and SE correlations with February temperatures were weaker (Figure 6a,b). At the same time, D_h of trees from SE, i.e. the higher and more southern sites were mostly positively correlated with average March–May temperature, while this relationship was not found for the other regions (Figure 6c,d).

Principal component gradient analyses indicated no species-specific effects on the observed gradient neither for LW nor for D_h when involving all tree and oak species (see Appendix S8). This observation was supported when applying PCGA only to data from sites (GOR/GOY and BRR/BRY) where two species co-existed (see Appendix S9).

3.4 | "Leave-one-out" analyses

The "leave-one-out" analysis indicated that most trees were correctly assigned to their specific site of origin based on LW and D_h (Table 3). That is, for LW 89% and 100% of eastern and western trees

were assigned correctly respectively. However, when analysing LW of only the eastern sites, no samples were assigned to the central east site. At the same time, D_h chronologies successfully detected samples coming from northeast (81%), central east (58%) or southeast (91%).
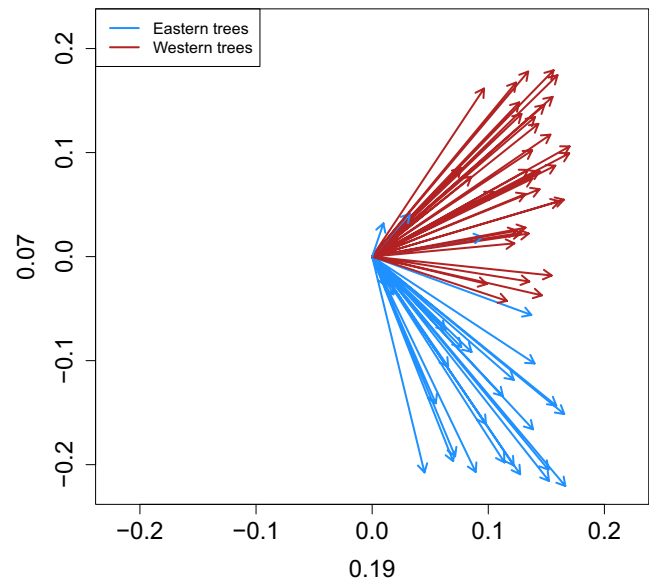

FIGURE 3 Loadings plot for the principal component gradient analyses based on latewood width. Each arrow represents the loadings on the first two principal components from one tree. Value labels on the *x*- and *y*-axes (0.19 and 0.07) represent the amount of explained variance by the respective component
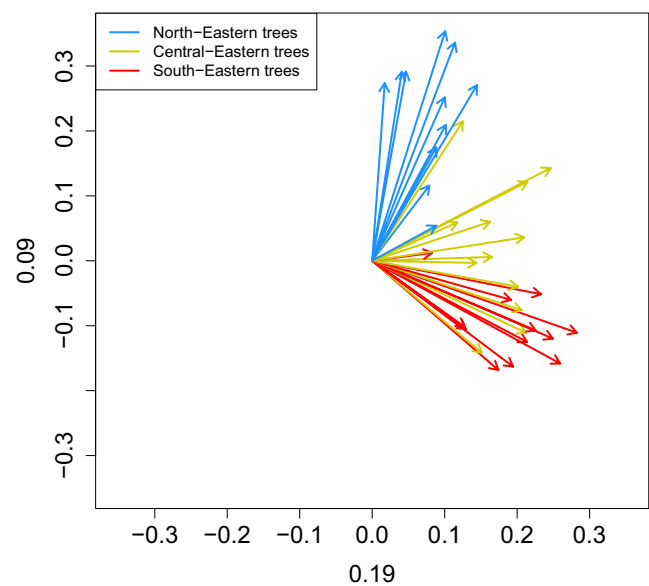
FIGURE 4 Loadings plot for the principal component gradient analyses based on hydraulic diameter but only considering the eastern sites. Each arrow represents the loadings on the first two principal components from one tree. Value labels on the *x*- and *y*-axes (0.19 and 0.09) represent the amount of explained variance by the respective component
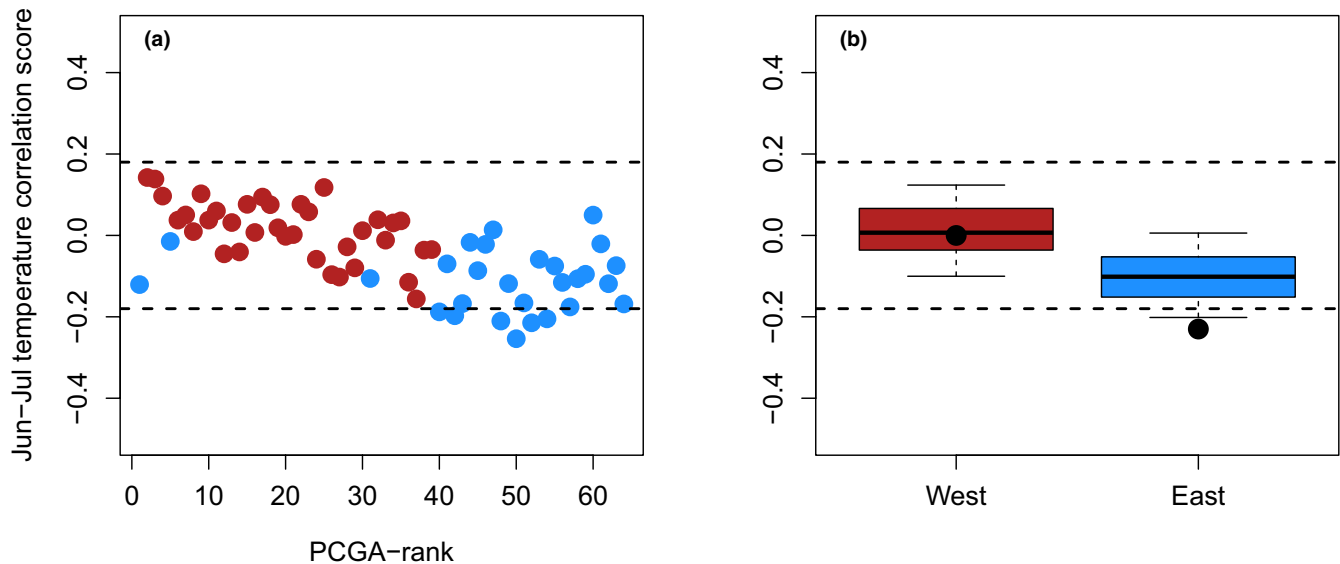
FIGURE 5 Relationships between climate correlations and the principal component gradient analyses (PCGA)-rank derived from latewood time series. (a) Correlations between latewood width time–series and average June–July temperatures for individual trees plotted against individual tree PCGA-ranks. PCGA-rank refers to the rank of a tree-ring series in the gradient defined by PCGA. (b) Correlations of individual tree latewood width series with average June–July temperature, separated according to geographic origin. Black dots in (b) represent the correlation coefficient of regional chronologies with average June–July temperature. Blue and red colors refer to eastern and western trees respectively. Note that the y-axes span the interval from −0.5 to 0.5

4 | DISCUSSION

4.1 | Added value of including complementary tree-ring variables into dendroprovenancing of oak

Our results indicate that a higher precision of provenancing can be achieved for ring-porous oak wood when combining wood-anatomical variables such as LW and size of EW-vessels, rather than using TRW (or LW) alone, as is usually the case in dendroprovenancing (e.g. Domínguez-Delmás et al., 2014; Haneca & Debonne, 2012). We found that annual variation patterns in LW and vessel D_h of the study species were related to the biogeographical origin, especially for D_h. Both variables are probably reflecting different climatic signals (winter and spring temperature for D_h, summer temperature for LW [Figures 4 and 5]), and therefore conditions during distinct periods of the year that largely determine the growth of oak in a specific area. LW allowed us to assign oaks to Basque (eastern) and Cantabrian (western) sites (Figure 3), whereas D_h discriminated oak populations across a latitude and elevation gradient (NE-CE-SE in Figure 4), which also represented increasing continentality. Thus, combining LW and D_h allows for resembling region-specific climate conditions over different parts of the growing season, which hence can be used to pinpoint the origin of wood.

The proposed combined approach is also interesting for other areas, such as the maritime part of Central Europe, where classical dendroprovenancing of oak fails (Bridge, 2000), probably due to its complex signal in TRW (Bridge, 2012). Moreover, TRW and LW of *Q. pyrenaica* in northwestern Spain were found to be influenced by forest dynamics, which is hardly the case for EW vessels (Souto-Herrero, Rozas, & García-González, 2018b). This is especially interesting for archaeological studies, as wood used for (ship-) construction often comes from managed forests.

Wood-anatomical analyses can also be applied to waterlogged timber, whereas there still is a knowledge gap about the change of wood composition under waterlogged or buried conditions. Isotopic analyses do not necessarily improve wood provenancing precision of living trees as well (Vlam et al., 2018), therefore they need to be further tested for different species and regions. However, isotopes might contain site-specific signals complementary to wood-anatomical variables (e.g. maximum summer temperature and precipitation in $\delta^{13}C$ and $\delta^{18}O$ in temperate regions [Treydte et al., 2007], strontium—reflects the soil signature [Hajj et al., 2017]). A combined multi-proxy dendroprovenancing method thus is the most promising approach for future studies. And integration with other techniques recently tested for dendroprovenancing, e.g. Fourier transform infrared spectroscopy (Traore, Kaal, & Cortizas, 2018), seems to broaden this potential.

Our results also demonstrate that a tree-centred approach, i.e. using single trees as a main source of information to understand variability in growth responses, as proposed for ecological studies (Sass-Klaassen et al., 2016) allows pin-pointing tree origin at both inter- and intra-regional scales. Such approach also overcomes the problem that often only few trees are available for dating and provenancing pieces of art (paintings, musical instruments, etc.).

4.2 | Spatial variation of climatic signal in different tree-ring variables

4.2.1 | Climatic signal in latewood width

Analyses of spatial variation of the climatic signal revealed that the main factor discriminating (based on LW time series) tree
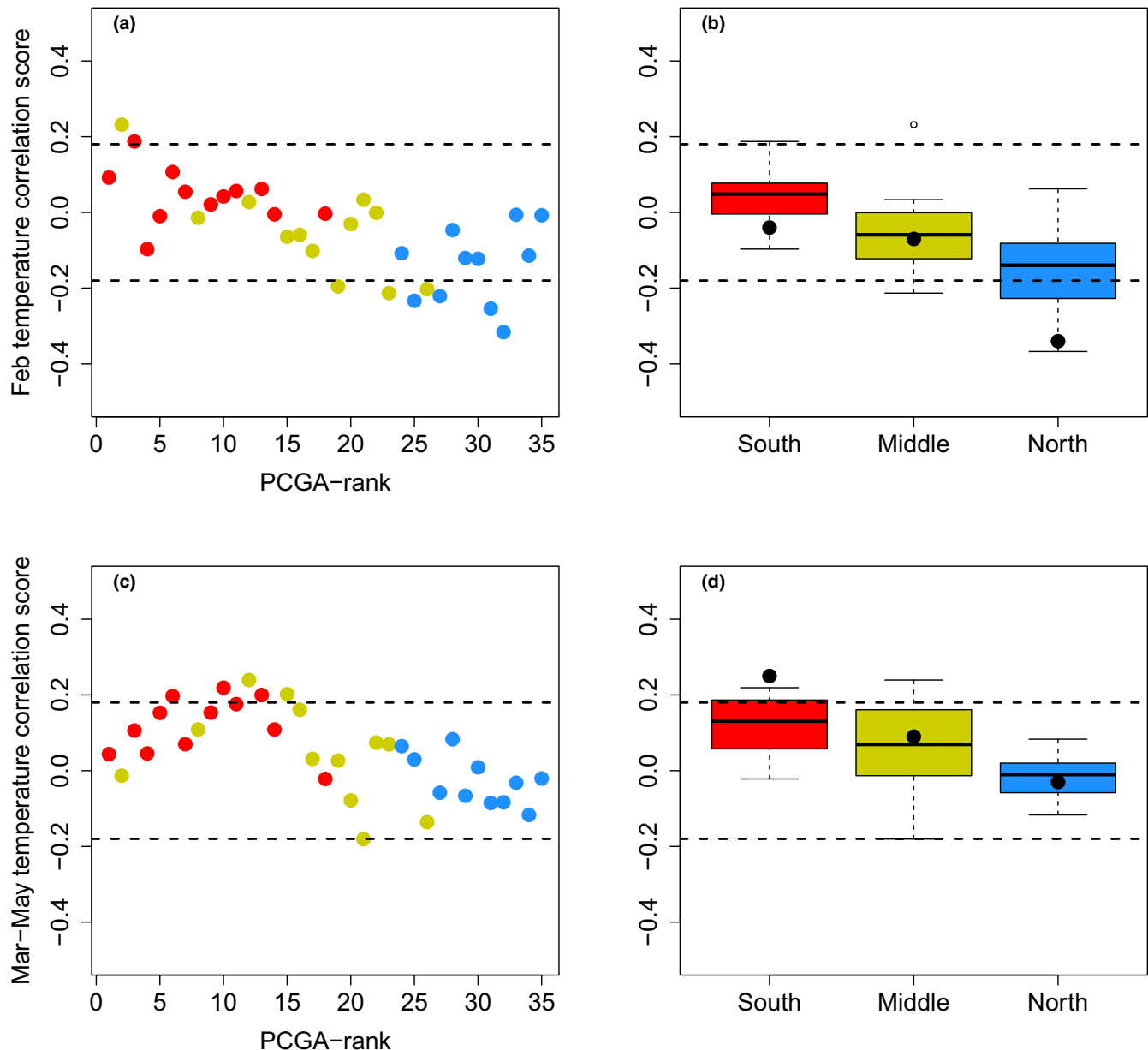
FIGURE 6 Relationships between climate correlations and the principal component gradient analyses (PCGA)-rank derived from hydraulic diameter (D_h) time series. (a) Correlations between individual tree ranks (from the PCGA) with correlation of individual tree D_h series and mean February temperature. (b) Correlations of individual tree D_h series with February temperature, black dots represent the average correlation coefficient (after bootstrapping) of regional chronologies with February temperature. (c) Correlations between individual tree ranks (from the PCGA) with correlation of individual tree D_h series and average March–May temperature. (d) Correlations of individual tree D_h series with average March–May temperature, with the black dot representing the average correlation coefficient (after bootstrapping) of regional chronologies with average March–May temperature. PCGA-rank in (a) and (c) refers to the rank of a D_h series in the gradient defined by PCGA. Blue, gold and red colors refer to trees from northeastern, central eastern and southeastern sites, respectively. Dashed lines indicate 0.05 significance thresholds. Note that the y-axes span the interval from −0.5 to 0.5

origin into Basque (eastern) and Cantabrian (western) sites was average June–July temperature (Figure 5a). The effect of average June–July temperature on tree growth was changing from no significant in the west to significantly negative in the east (Figure 5b, see Appendix S10) with the signal mostly driven by the lowest and highest sites. In general, radial growth of deciduous oaks in the Mediterranean is negatively related to high temperature during summer (Rozas, 2001, 2005; Souto-Herrero et al., 2018b; Tessier,

Nola, & Serrebachet, 1994), i.e. the period with maximum growth activity (Castagneri, Regev, Boaretto, & Carrer, 2017). High summer temperature increases drought stress due to elevated evapotranspiration, leading to reduction of photosynthesis, favouring reserve storage and consequently slowing of growth rates (Bréda et al., 2006; Sala, Woodruff, & Meinzer, 2012). In contrast to oaks from Basque (eastern sites), trees from Cantabria (western sites) did not show any significant response to summer temperature (Figure 5b).

TABLE 3   Rates of success for the leave one out approach. West, East indicate success rates of assigning trees to eastern and western sites, respectively. NE, CE and SE indicate success rates of assigning trees to north, central and southeastern sites, respectively. For the latter, only trees from eastern sites were used

	West	East	NE	CE	SE
LW	100%	89%	81%	0%	100%
D_h	61%	35%	81%	58%	91%

The lack of summer signal was observed before in oaks growing in Northern Spain under an Atlantic climate, and was explained by forest dynamics, i.e. disturbances and management activities resulting in abrupt growth changes which probably masked the effect of climate (Souto-Herrero et al., 2018a, 2018b). At the same time, LW of trees both from eastern and western regions showed positive correlations with summer precipitation (see Appendix S11), a common signal for the southeast of Central Europe (Čufar et al., 2014) and the Mediterranean region (Nola, 1996; Tessier et al., 1994).

4.2.2 | Climatic signal in earlywood vessels across a latitudinal/topographic gradient

The grouping of the oaks growing in the Basque country (eastern sites) into a northern (NE), central (CE) and southern (SE) group was reflected in a varying response of D_h to temperature in February and March–May (Figure 6). Although oak trees initiate cambial division in February/middle March (see Pérez-de-Lis et al. (2016) and González-González, García-González, and Vazquez-Ruiz (2013) for *Q. robur* and *Q. pyrenaica*), high winter temperatures are apparently related to the formation of smaller vessels. This effect was strongest in oaks from NE, and has been reported earlier for *Castanea* sativa Mill. in the Swiss Alps (Fonti & García-González, 2004; Fonti et al., 2007) and for *Quercus petraea* and *Q. pyrenaica* from Northern Iberia (González-González et al., 2014). A negative February temperature effect has been previously explained by the temperature sensitivity to the plant hormone auxin (Fonti et al., 2007), which controls the cambial activity and is involved in vascular differentiation (Fukuda, 2004; Kepinski, 2006). High winter temperature is assumed to increase cell sensitivity to auxin, resulting in an earlier and faster process of vessel differentiation, which leads to the formation of smaller vessels (Aloni & Zimmermann, 1983). This temperature effect on vessel size can also be attributed to carbohydrate dynamics. Higher winter temperatures enhance respiration rates and thus can lead to the depletion of assimilates stored. As cambial resumption of ring-porous oaks starts before bud break (Copini et al., 2016; Kudo et al., 2014; Pérez-de-Lis et al., 2016), and vessel functionality occurs just before the leaf expansion (Guada, García-González, Pérez-de-Lis, Vázquez-Ruiz, & Montserrat-Martí, 2018; Kitin & Funada, 2016) the formation of EW vessels relies on the amount of stored carbohydrates from the previous growing season. A shortage of carbohydrates as an effect of high winter temperatures can therefore be associated with the formation of smaller vessels (González-González, Vazquez-Ruiz,

& García-González, 2015). In contrast, high average temperatures during March–May have a positive effect on vessel size at the southeastern (the most inland) sites. During spring, warmer conditions are known to foster bud break, and thus produce new sources of auxin (Sorce, Giovannelli, Sebastiani, & Anfodillo, 2013) to be transported along the stem, so that cambial activity is initiated (Schrader et al., 2003) thereby favouring vessel expansion (Uggla, Moritz, Sandberg, & Sundberg, 1996).

4.3 | Species effect on variation of selected tree-ring variables

The ring-porous oak species used in this study are very similar if not identical in their wood structure (Crivellaro et al., 2013; Schweingruber & Baas, 1990) but differ in their ecology, and consequently in their geographical distribution. However, this difference was not reflected in the variation of their ring width and vessel size patterns as indicated by the PCGA (see Appendix S8), which shows an overriding effect of site-specific conditions. It is evident that differences in species ecology determine their distribution in the study area, which is probably the reason why we did not find sites where all four species coexist. In fact, the two sub-Mediterranean oaks (*Q. pyrenaica* and *Q. faginea*), apparently the most xeric species, could not be compared to each other because they have opposite soil requirements (acidic and basic respectively). Therefore, we could only check for species-specific differences on two coexisting species (*Q. petraea* and *Q. pyrenaica*) at two study sites.

Our results support the impression that both ring width and vessel size respond more to specific site conditions than to genetic background (see Appendix S9). Furthermore, at both sites where we could compare two species, one of them was *Q. pyrenaica*. This is a sub-Mediterranean mountain species, with specific adaptations to these drier environments: xerophytic leaf habit, late flushing, and a more conservative wood formation strategy compared to nemoral oak species (Pérez de Lis et al., 2016). Despite these differences, its growth responses were similar to those of the other species occurring at the same sites. This is in contrast with previous works comparing nemoral and sub-Mediterranean oaks at the same site, where species-specific responses were observed (González-González et al., 2014).

The inclusion of wood anatomical features and their directional and plausible climate responses across biogeographical gradients allow for more precise provenancing of oak wood in Northern Spain. These results are probably extendable to other areas, and a larger set of species and wood anatomical proxies (e.g. wood density [Wilson et al., 2017]; parenchyma fractions [Morris et al., 2018]) should be explored. Moreover, as ring-porous oak species in Northern Spain exhibit specific biogeographical distributions, integration of DNA analyses for species identification or genome sequencing (Schroeder et al., 2016) could further supplement the tool-box for dendroprovenancing. We believe that with a multi-variable approach we achieve a higher precision in dendroprovenancing and pinpoint origin of timber on a finer scale.

5 | CONCLUSION & OUTLOOK

We showed that a novel approach—comprising multiple variables (LW and vessel area) and combining multivariate techniques (PCGA) with statistical validation procedures (leave-one-out)—can increase the precision of pin-pointing the origin of oak timber. Further studies emphasizing on other regions, species (e.g. coniferous trees), and tree-ring variables (e.g. stable isotopes, wood density) are however needed to extend our knowledge on the ability of this approach to the refine dendroprovenancing. In addition, an individual tree-based approach may reveal more insights into spatial variations of climate–growth relationships, most likely depending on specific site conditions.

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REFERENCES

Aloni, R., & Zimmermann, M. H. (1983). The control of vessel size and density along the plant axis - a new hypothesis. *Differentiation*, *24*, 203–208. https://doi.org/10.1111/j.1432-0436.1983.tb01320.x

Amaral Franco, J. (1990). *Quercus* L. *Flora Ibérica*. In S. Castroviejo, M. Laínz, G. López González, P. Montserrat, F. Muñoz Garmendia, J. Paiva, & L. Villar (Eds.), pp. 15–36. Madrid, Spain.

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., ... Frank, D. (2013). Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, *22*, 706–717. https://doi.org/10.1111/geb.12023

Billamboz, A. (2003). Tree rings and wetland occupation in Southwest Germany between 2000 and 500 BC: Dendroarchaeology beyond dating in tribute to F. H. Schweingruber. *Tree-Ring Research*, *59*, 37–49.

Blanco Castro, E., Casado González, M. A., Costa Tenorio, M., Escribano Bombín, R., Garcia Antón, M., Genova Fuster, M., ... Sainz Ollero, H. (2005). Los bosques ibéricos. Una interpretación geobotánica.

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*, 625–644. https://doi.org/10.1051/forest:2006042

Bridge, M. (2000). Can dendrochronology be used to indicate the source of oak within Britain? *Vernacular Architecture*, *31*(1), 67–72. https://doi.org/10.1179/vea.2000.31.1.67

Bridge, M. (2011). Resource exploitation and wood mobility in Northern European Oak: Dendroprovenancing of individual timbers from the Mary Rose (1510/11-1545). *International Journal of Nautical Archaeology*, *40*, 417–423. https://doi.org/10.1111/j.1095-9270.2010.00309.x

Bridge, M. (2012). Locating the origins of wood resources: A review of dendroprovenancing. *Journal of Archaeological Science*, *39*, 2828–2834. https://doi.org/10.1016/j.jas.2012.04.028

Bunn, A. G. (2010). Statistical and visual crossdating in R using the dplR library. *Dendrochronologia*, *28*, 251–258. https://doi.org/10.1016/j.dendro.2009.12.001

Buras, A., der, van Maaten-Theunissen, M., der, van Maaten, E., Ahlgrimm, S., Hermann, P., & Simard, S., ... Wilmking, M. (2016). Tuning the voices of a choir: Detecting ecological gradients in time-series populations. *PLoS ONE*, *11*, e0158346. https://doi.org/10.1371/journal.pone.0158346

Castagneri, D., Regev, L., Boaretto, E., & Carrer, M. (2017). Xylem anatomical traits reveal different strategies of two Mediterranean oaks to cope with drought and warming. *Environmental and Experimental Botany*, *133*, 128–138. https://doi.org/10.1016/j.envexpbot.2016.10.009

Castro, F. (2008). In search of unique Iberian ship design concepts. *Historical Archaeology*, *42*, 63–87. https://doi.org/10.1007/BF03377074

Chen, K., Dorado-Liñán, I., Akhmetzyanov, L., Gea-Izquierdo, G., Zlatanov, T., & Menzel, A. (2015). Influence of climate drivers and the North Atlantic Oscillation on beech growth at marginal sites across the Mediterranean. *Climate Research*, *66*, 229–242. https://doi.org/10.3354/cr01345

Cook, E., Briffa, K., Shiyatov, S., & Mazepa, V. (1992). Tree-ring standardization and growth trend estimation. In E. R. Cook & L. A. Kairiukstis (Eds.), *Methods of dendrochronology: Application in the environmental science* (pp. 104–122). Dordrecht, The Netherlands: Kluwer Academic Publisher.

Copini, P., den Ouden, J., Robert, E. M. R., Tardif, J. C., Loesberg, W. A., Goudzwaard, L., & Sass-Klaassen, U. (2016). Flood-ring formation and root development in response to experimental flooding of young *Quercus robur* trees. *Frontiers in Plant Science*, *7*.

Crivellaro, A., Schweingruber, F. H., Christodoulou, C. S., Papachristophorou, T., Tsintides, T., & Da Ros, A.; Ohio Library and Information Network. (2013). Atlas of wood, bark and pith anatomy of Eastern Mediterranean trees and shrubs: with a special focus on Cyprus. pp. 1 online resource (xii, 583 pages).

Čufar, K., De Luis, M., Zupančič, M., & Eckstein, D. (2008). A 548-year tree-ring chronology of oak (*Quercus* spp.) for southeast Slovenia and its significance as a dating tool and climate archive. *Tree-Ring Research*, *64*, 3–15.

Čufar, K., Grabner, M., Morgós, A., del Castillo, E. M., Merela, M., & de Luis, M. (2014). Common climatic signals affecting oak tree-ring growth in SE Central Europe. *Trees-Structure and Function*, *28*, 1267–1277.

de Luis, M., Novak, K., Raventós, J., Gričar, J., Prislan, P., & Čufar, K. (2011). Climate factors promoting intra-annual density fluctuations in Aleppo pine (*Pinus halepensis*) from semiarid sites. *Dendrochronologia*, *29*, 163–169. https://doi.org/10.1016/j.dendro.2011.01.005

Domínguez-Delmás, M., Alejano-Monge, R., Van Daalen, S., Rodríguez-Trobajo, E., García-González, I., Susperregi, J., … Jansma, E. (2015). Tree-rings, forest history and cultural heritage: Current state and future prospects of dendroarchaeology in the Iberian Peninsula. *Journal of Archaeological Science*, *57*, 180–196. https://doi.org/10.1016/j.jas.2015.02.011

Domínguez-Delmás, M., Driessen, M., García-González, I., van Helmond, N., Visser, R., & Jansma, E. (2014). Long-distance oak supply in mid-2nd century AD revealed: The case of a Roman harbour (Voorburg-Arentsburg) in the Netherlands. *Journal of Archaeological Science*, *41*, 642–654. https://doi.org/10.1016/j.jas.2013.09.009

Domínguez-Delmás, M., Nayling, N., Ważny, T., Loureiro, V., & Lavier, C. (2013). Dendrochronological dating and provenancing of timbers from the arade 1 Shipwreck, Portugal. *International Journal of Nautical Archaeology*, *42*, 118–136. https://doi.org/10.1111/j.1095-9270.2012.00361.x

Dorado-Liñán, I., Akhmetzyanov, L., & Menzel, A. (2017). Climate threats on growth of rear-edge European beech peripheral populations in Spain. *International Journal of Biometeorology*, *61*, 2097–2110. https://doi.org/10.1007/s00484-017-1410-5

Eaton, E., Caudillo, G., Oliveira, S., & de, Rigo, D. (2016). *Quercus robur* and *Quercus petraea* in Europe: Distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. De Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European atlas of forest tree species* (pp. 160–163). Luxembourg: Publication Office of the European Union.

Esteban, L. G., Martin, J. A., de Palacios, P., & Fernandez, F. G. (2012). Influence of region of provenance and climate factors on wood anatomical traits of *Pinus nigra* Arn. subsp *salzmannii*. *European Journal of Forest Research*, *131*, 633–645. https://doi.org/10.1007/s10342-011-0537-x

Fonti, P., & García-González, I. (2004). Suitability of chestnut earlywood vessel chronologies for ecological studies. *New Phytologist*, *163*, 77–86. https://doi.org/10.1111/j.1469-8137.2004.01089.x

Fonti, P., Solomonoff, N., & García-González, I. (2007). Earlywood vessels of *Castanea sativa* record temperature before their formation. *New Phytologist*, *173*, 562–570. https://doi.org/10.1111/j.1469-8137.2006.01945.x

Fowler, A. M., & Bridge, M. C. (2017). Empirically-determined statistical significance of the Baillie and Pilcher (1973) t statistic for British Isles oak. *Dendrochronologia*, *42*, 51–55. https://doi.org/10.1016/j.dendro.2016.12.006

Fritts, H. C. (1976). *Tree rings and climate*. London, UK: Academic Press.

Fukuda, H. (2004). Signals that control plant vascular cell differentiation. *Nature Reviews Molecular Cell Biology*, *5*, 379–391. https://doi.org/10.1038/nrm1364

García-González, I., & Fonti, P. (2006). Selecting earlywood vessels to maximize their environmental signal. *Tree Physiology*, *26*, 1289–1296. https://doi.org/10.1093/treephys/26.10.1289

García-González, I., Souto-Herrero, M., & Campelo, F. (2016). Ring-porosity and earlywood vessels: A review on extracting environmental information through time. *Iawa Journal*, *37*, 295–314. https://doi.org/10.1163/22941932-20160135

Gärtner, H., & Nievergelt, D. (2010). The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia*, *28*, 85–92. https://doi.org/10.1016/j.dendro.2009.09.002

Gazol, A., Camarero, J. J., Anderegg, W. R. L., & Vicente-Serrano, S. M. (2017). Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Global Ecology and Biogeography*, *26*, 166–176. https://doi.org/10.1111/geb.12526

González-González, B. D., García-González, I., & Vazquez-Ruiz, R. A. (2013). Comparative cambial dynamics and phenology of *Quercus robur* L. and Q-pyrenaica Willd. in an Atlantic forest of the northwestern Iberian Peninsula. *Trees-Structure and Function*, *27*, 1571–1585. https://doi.org/10.1007/s00468-013-0905-x

González-González, B. D., Rozas, V., & García-González, I. (2014). Earlywood vessels of the sub-Mediterranean oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q. petraea* at the Atlantic-Mediterranean boundary. *Trees-Structure and Function*, *28*, 237–252. https://doi.org/10.1007/s00468-013-0945-2

González-González, B. D., Vazquez-Ruiz, R. A., & García-González, I. (2015). Effects of climate on earlywood vessel formation of *Quercus robur* and *Q. pyrenaica* at a site in the northwestern Iberian Peninsula. *Canadian Journal of Forest Research*, *45*, 698–709. https://doi.org/10.1139/cjfr-2014-0436

Gori, Y., Wehrens, R., La Porta, N., & Camin, F. (2015). Oxygen and hydrogen stable isotope ratios of bulk needles reveal the geographic origin of Norway spruce in the European Alps. *PLoS ONE*, *10*, e0118941. https://doi.org/10.1371/journal.pone.0118941

Gričar, J., de Luis, M., Hafner, P., & Levanič, T. (2013). Anatomical characteristics and hydrologic signals in tree-rings of oaks (*Quercus robur* L.). *Trees-Structure and Function*, *27*, 1669–1680.

Grissino-Mayer, H. D. (2001). Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, *57*, 205–221.

Grudd, H. (2008). Tornetrask tree-ring width and density AD 500-2004: A test of climatic sensitivity and a new 1500-year reconstruction of north Fennoscandian summers. *Climate Dynamics*, *31*, 843–857. https://doi.org/10.1007/s00382-007-0358-2

Guada, G., García-González, I., Pérez-de-Lis, G., Vázquez-Ruiz, R. A., & Montserrat-Martí, G. (2018). Dry matter content during extension of twigs, buds and leaves reflects hydraulic status related to earlywood vessel development in *Quercus pyrenaica* Willd. *European Journal of Forest Research*, *137*, 307–319. https://doi.org/10.1007/s10342-018-1104-5

Gutiérrez, A. G., Snell, R. S., & Bugmann, H. (2016). Using a dynamic forest model to predict tree species distributions. *Global Ecology and Biogeography*, *25*, 347–358. https://doi.org/10.1111/geb.12421

Hajj, F., Poszwa, A., Bouchez, J., & Guerold, F. (2017). Radiogenic and "stable" strontium isotopes in provenance studies: A review and first results on archaeological wood from shipwrecks. *Journal of Archaeological Science*, *86*, 24–49. https://doi.org/10.1016/j.jas.2017.09.005

Haneca, K., Boeren, I., Van Acker, J., & Beeckman, H. (2006). Dendrochronology in suboptimal conditions: Tree rings from medieval oak from Flanders (Belgium) as dating tools and archives of past forest management. *Vegetation History and Archaeobotany*, *15*, 137–144. https://doi.org/10.1007/s00334-005-0022-x

Haneca, K., Čufar, K., & Beeckman, H. (2009). Oaks, tree-rings and wooden cultural heritage: A review of the main characteristics and applications of oak dendrochronology in Europe. *Journal of Archaeological Science*, *36*, 1–11. https://doi.org/10.1016/j.jas.2008.07.005

Haneca, K., & Debonne, V. (2012). Precise tree-ring dating of building activities despite the absence of bark: A case-study on medieval church roofs in Damme, Belgium. *Dendrochronologia*, *30*, 23–34. https://doi.org/10.1016/j.dendro.2011.06.002

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, *34*, 623–642. https://doi.org/10.1002/joc.3711

Holz, A., Hart, S. J., Williamson, G. J., Veblen, T. T., & Aravena, J. C. (2018). Radial growth response to climate change along the latitudinal range of the world's southernmost conifer in southern South America. *Journal of Biogeography*, *45*, 1140–1152. https://doi.org/10.1111/jbi.13199

Horacek, M. (2012). Christmas tree production in Europe: Control of declared geographical origin by stable isotope analysis – a pilot study. *Die Bodenkultur*, *63*, 35–41.

Horacek, M., Jakusch, M., & Krehan, H. (2009). Control of origin of larch wood: Discrimination between European (Austrian) and Siberian origin by stable isotope analysis. *Rapid Communications in Mass Spectrometry*, *23*, 3688–3692. https://doi.org/10.1002/rcm.4309

Jiménez Sancho, M. P., Díaz Fernández, P. M., Martín Albertos, S., & Gil Sánchez, L. (1998). *Regiones de procedencia: Quercus pyrenaica Willd., Quercus faginea Lam. y Quercus canariensis Willd*. Madrid, Spain: OAPN.

Kagawa, A., & Leavitt, S. W. (2010). Stable carbon isotopes of tree rings as a tool to pinpoint the geographic origin of timber. *Journal of Wood Science*, *56*, 175–183. https://doi.org/10.1007/s10086-009-1085-6

Kepinski, S. (2006). Integrating hormone signaling and patterning mechanisms in plant development. *Current Opinion in Plant Biology*, *9*, 28–34. https://doi.org/10.1016/j.pbi.2005.11.001

Kitin, P., & Funada, R. (2016). Earlywood vessels in ring-porous trees become functional for water transport after bud burst and before the maturation of the current-year leaves. *Iawa Journal*, *37*, 315–331. https://doi.org/10.1163/22941932-20160136

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, *31*, 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x

Kudo, K., Nabeshima, E., Begum, S., Yamagishi, Y., Nakaba, S., Oribe, Y., … Funada, R. (2014). The effects of localized heating and disbudding on cambial reactivation and formation of earlywood vessels in seedlings of the deciduous ring-porous hardwood, *Quercus serrata*. *Annals of Botany*, *113*, 1021–1027. https://doi.org/10.1093/aob/mcu026

Martin-Benito, D., Beeckman, H., & Cañellas, I. (2013). Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest. *European Journal of Forest Research*, *132*, 33–45. https://doi.org/10.1007/s10342-012-0652-3

Martin-Benito, D., & Pederson, N. (2015). Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *Journal of Biogeography*, *42*, 925–937. https://doi.org/10.1111/jbi.12462

Martínez Ruiz, E. (1999). Los montes en la cultura islámica. El bosque de al-Andalus desde el siglo VIII al XIII. *Collectanea*, *27*, 63–87.

McCarroll, D., Loader, N. J., Jalkanen, R., Gagen, M. H., Grudd, H., Gunnarson, B. E., … Zorita, E. (2013). A 1200-year multiproxy record of tree growth and summer temperature at the northern pine forest limit of Europe. *Holocene*, *23*, 471–484. https://doi.org/10.1177/0959683612467483

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., … Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Morris, H., Gillingham, M. A. F., Plavcová, L., Gleason, S. M., Olson, M. E., Coomes, D. A., … Jansen, S. (2018). Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. *Plant, Cell & Environment*, *41*, 245–260. https://doi.org/10.1111/pce.13091

Nieto Quintano, P., Caudillo, G., & de, Rigo, D. (2016). *Quercus pyrenaica* in Europe: Distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. De Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European atlas of forest tree species* (pp ee01f807). Luxembourg: Publication Office of the European Union.

Nola, P. (1996). Climatic signal in earlywood and latewood of deciduous oaks from northern Italy. In J. S. Dean, D. M. Meko, & T. W. Swetnam (Eds.), *Tree rings, environment, and humanity* (pp. 149–258). Tucson, AZ: University of Arizona.

Olano, J. M., Linares, J. C., García-Cervigón, A. I., Arzac, A., Delgado, A., & Rozas, V. (2014). Drought-induced increase in water-use efficiency reduces secondary tree growth and tracheid wall thickness in a Mediterranean conifer. *Oecologia*, *176*, 273–283. https://doi.org/10.1007/s00442-014-2989-4

Pérez-de-Lis, G., Rossi, S., Vazquez-Ruiz, R. A., Rozas, V., & García-González, I. (2016). Do changes in spring phenology affect earlywood vessels? Perspective from the xylogenesis monitoring of two sympatric ring-porous oaks. *New Phytologist*, *209*, 521–530. https://doi.org/10.1111/nph.13610

Petit, G., Anfodillo, T., Carraro, V., Grani, F., & Carrer, M. (2011). Hydraulic constraints limit height growth in trees at high altitude. *New Phytologist*, *189*, 241–252. https://doi.org/10.1111/j.1469-8137.2010.03455.x

R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Revelle, W. (2017). *psych: Procedure for personality and psychological research*. Evanston, IL: Northwestern University.

Rich, S., Manning, S. W., Degryse, P., Vanhaecke, F., Latruwe, K., & Van Lerberghe, K. (2016). To put a cedar ship in a bottle: Dendroprovenancing three ancient East Mediterranean watercraft with the Sr-87/Sr-86 isotope ratio. *Journal of Archaeological Science-Reports*, *9*, 514–521. https://doi.org/10.1016/j.jasrep.2016.08.034

Rozas, V. (2001). Detecting the impact of climate and disturbances on tree-rings of *Fagus sylvatica* L. and *Quercus robur* L. in a lowland forest in Cantabria. *Northern Spain. Annals of Forest Science*, *58*, 237–251. https://doi.org/10.1051/forest:2001123

Rozas, V. (2005). Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: Tree-ring growth responses to climate. *Annals of Forest Science*, *62*, 209–218. https://doi.org/10.1051/forest:2005012

Rydval, M., Gunnarson, B. E., Loader, N. J., Cook, E. R., Druckenbrod, D. L., & Wilson, R. (2017). Spatial reconstruction of Scottish summer temperatures from tree rings. *International Journal of Climatology*, *37*, 1540–1556. https://doi.org/10.1002/joc.4796

Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? *Tree Physiology*, *32*, 764–775. https://doi.org/10.1093/treephys/tpr143

Sass-Klaassen, U., Fonti, P., Cherubini, P., Gričar, J., Robert, E. M. R., Steppe, K., & Bräuning, A. (2016). A tree-centered approach to assess impacts of extreme climatic events on forests. *Front Plant Sci*, *7*, 1069.

Sass-Klaassen, U., Vernimmen, T., & Baittinger, C. (2008). Dendrochronological dating and provenancing of timber used as foundation piles under historic buildings in the Netherlands. *International Biodeterioration & Biodegradation*, *61*, 96–105. https://doi.org/10.1016/j.ibiod.2007.07.013

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675. https://doi.org/10.1038/nmeth.2089

Schofield, M. R., Barker, R. J., Gelman, A., Cook, E. R., & Briffa, K. R. (2016). A model-based approach to climate reconstruction using tree-ring data. *Journal of the American Statistical Association*, *111*, 93–106. https://doi.org/10.1080/01621459.2015.1110524

Schrader, J., Baba, K., May, S. T., Palme, K., Bennett, M., Bhalerao, R. P., & Sandberg, G. (2003). Polar auxin transport in the wood-forming tissues of hybrid aspen is under simultaneous control of developmental and environmental signals. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 10096–10101. https://doi.org/10.1073/pnas.1633693100

Schroeder, H., Cronn, R., Yanbaev, Y., Jennings, T., Mader, M., Degen, B., & Kersten, B. (2016). Development of molecular markers for determining continental origin of wood from white oaks (*Quercus* L. sect. *Quercus*). *PLoS ONE*, *11*, e0158221. https://doi.org/10.1371/journal.pone.0158221

Schweingruber, F. H., & Baas, P. (1990). *Anatomie europäischer Hölzer ein Atlas zur Bestimmung europäischer Baum-, Strauch- und Zwergstrauchhölzer*. Bern, Switzerland: Haupt.

Sorce, C., Giovannelli, A., Sebastiani, L., & Anfodillo, T. (2013). Hormonal signals involved in the regulation of cambial activity, xylogenesis and vessel patterning in trees. *Plant Cell Reports*, 32, 885–898. https://doi.org/10.1007/s00299-013-1431-4

Souto-Herrero, M., Rozas, V., & García-González, I. (2017). A 481-year chronology of oak earlywood vessels as an age-independent climatic proxy in NW Iberia. *Global and Planetary Change*, 155, 20–28. https://doi.org/10.1016/j.gloplacha.2017.06.003

Souto-Herrero, M., Rozas, V., & García-González, I. (2018a). Chronologies of earlywood vessels and latewood width disentangle climate drivers of oak growth in a mild oceanic region. *Dendrochronologia*, 51, 40–53. https://doi.org/10.1016/j.dendro.2018.07.004

Souto-Herrero, M., Rozas, V., & García-González, I. (2018b). Earlywood vessels and latewood width explain the role of climate on wood formation of *Quercus pyrenaica* Willd. across the Atlantic-Mediterranean boundary in NW Iberia. *Forest Ecology and Management*, 425, 126–137. https://doi.org/10.1016/j.foreco.2018.05.042

Speer, J. H. (2010). *Fundamentals of tree-ring research*. Tucson, AZ: University of Arizona Press.

Sperry, J. S., Nichols, K. L., Sullivan, J. E. M., & Eastlack, S. E. (1994). Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of Northern Utah and interior Alaska. *Ecology*, 75, 1736–1752. https://doi.org/10.2307/1939633

Tegel, W., Elburg, R., Hakelberg, D., Stäuble, H., & Büntgen, U. (2012). Early neolithic water wells reveal the world's oldest wood architecture. *PLoS ONE*, 7, e51374. https://doi.org/10.1371/journal.pone.0051374

Tessier, L., Nola, P., & Serrebachet, F. (1994). Deciduous *Quercus* in the Mediterranean region - tree-ring/climate relationships. *New Phytologist*, 126, 355–367. https://doi.org/10.1111/j.1469-8137.1994.tb03955.x

Traore, M., Kaal, J., & Cortizas, A. M. (2018). Differentiation between pine woods according to species and growing location using FTIR-ATR. *Wood Science and Technology*, 52, 487–504. https://doi.org/10.1007/s00226-017-0967-9

Treydte, K., Frank, D., Esper, J., Andreu, L., Bednarz, Z., & Berninger, F., … Schleser, G. H. (2007). Signal strength and climate calibration of a European tree-ring isotope network. *Geophysical Research Letters*, 34, L24302. https://doi.org/10.1029/2007GL031106

Uggla, C., Moritz, T., Sandberg, G., & Sundberg, B. (1996). Auxin as a positional signal in pattern formation in plants. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 9282–9286. https://doi.org/10.1073/pnas.93.17.9282

van der Maaten, E., Hamann, A., van der Maaten-Theunissen, M., Bergsma, A., Hengeveld, G., van Lammeren, R., … Sterck, F. (2017). Species distribution models predict temporal but not spatial variation in forest growth. *Ecology and Evolution*, 7, 2585–2594. https://doi.org/10.1002/ece3.2696

Vicente-Serrano, S. M., Camarero, J. J., & Azorin-Molina, C. (2014). Diverse responses of forest growth to drought time-scales in the Northern Hemisphere. *Global Ecology and Biogeography*, 23, 1019–1030. https://doi.org/10.1111/geb.12183

Vlam, M., de Groot, G. A., Boom, A., Copini, P., Laros, I., Veldhuijzen, K., … Zuidema, P. A. (2018). Developing forensic tools for an African timber: Regional origin is revealed by genetic characteristics, but not by isotopic signature. *Biological Conservation*, 220, 262–271. https://doi.org/10.1016/j.biocon.2018.01.031

von Arx, G., & Carrer, M. (2014). ROXAS - A new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia*, 32, 290–293. https://doi.org/10.1016/j.dendro.2013.12.001

Ważny, T. (2002). Baltic timber in Western Europe – an exciting dendrochronological question. *Dendrochronologia*, 20, 313–320.

Williams, A. P., Michaelsen, J., Leavitt, S. W., & Still, C. J. (2010). Using tree rings to predict the response of tree growth to climate change in the continental United States during the twenty-first century. *Earth Interactions*, 14, 1–20. https://doi.org/10.1175/2010EI362.1

Wilson, R., Wilson, D., Rydval, M., Crone, A., Büntgen, U., Clark, S., … Mills, C. (2017). Facilitating tree-ring dating of historic conifer timbers using Blue Intensity. *Journal of Archaeological Science*, 78, 99–111. https://doi.org/10.1016/j.jas.2016.11.011

Yang, B., He, M. H., Melvin, T. M., Zhao, Y., & Briffa, K. R. (2013). Climate control on tree growth at the upper and lower treelines: A case study in the Qilian Mountains, Tibetan Plateau. *PLoS ONE*, 8, e69065. https://doi.org/10.1371/journal.pone.0069065

Zang, C., & Biondi, F. (2015). treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38, 431–436. https://doi.org/10.1111/ecog.01335

BIOSKETCH

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SUPPORTING INFORMATION

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