Constrained trait variation by water availability modulates radial growth in evergreen and deciduous Mediterranean oaks

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ABSTRACT

Spatial and temporal variation in functional traits allows trees to adjust to shifting environmental conditions such as water stress. However, the change of traits, both mean and variances, along water availability gradients and across growing seasons, as well as their covariation with tree performance, have been rarely assessed. We examined intraspecific trait variation in coexisting evergreen (*Quercus ilex* ssp. *ilex* and *Q. ilex* ssp. *ballota*) and deciduous (*Quercus faginea* and *Quercus humilis*) Mediterranean oaks along a wide water availability gradient in northeastern Spain during six years. We measured leaf area (LA), shoot twig mass (Sm), leaf mass per area (LMA) and the ratio of shoot twig to leaf biomass (Sm:Lm). We characterized tree performance through basal area increment (BAI) and drought resilience indices. Higher variation was found within individuals than between individuals across populations and years. Within species, we found trait adjustments toward more conservative water-use (low LA and Sm and high LMA) with increasing drier conditions. Intraspecific trait variation was constrained by water availability, particularly on the deciduous species. In *Q. ilex*, trait variance of LMA positively covaried with annual BAI, whereas variance of LA, Sm and Sm:Lm was positively related to resistance and resilience against the severe 2012 drought in deciduous oaks. Our results support a tradeoff between the ability to tolerate drought and the capacity to cope with unpredictable changes in the environment through increased intraspecific trait variation, which may have implications on tree performance in the face of increased extreme events.

1. Introduction

The ability of tree species to adjust to new environmental conditions directly or indirectly relies on the variability in their morpho-physio-phenological attributes, that is, their functional traits (Violle et al., 2007). Temperature and the frequency and intensity of severe climate extremes such as droughts and heatwaves are expected to increase according to model-based climate projections for the 21st century (Zhou et al., 2019; IPCC, 2021). This will modify forest functioning, potentially inducing tree species migration and extinction (Jump and Peñuelas, 2005; Seidl et al., 2017). Therefore, a better understanding of the source of functional trait variation, along with the linkages between tree fitness and functional traits will greatly improve our capacity to model and predict forest responses under changing conditions.

Many studies have applied a trait-based approach focused on mean species trait values (e.g., Anderegg et al., 2016; Serra-Maluquer et al.,

2022). However, there is increasing evidence that intraspecific trait variation (ITV) is substantial and it is relevant for population dynamics and ecosystem processes (Westerband et al., 2021), particularly for species widely distributed along environmental gradients (Fajardo and Piper, 2011; Anderegg, 2015; Siefert et al., 2015; Rosas et al., 2019). Trait variability is structured across aggregated ecological scales, driven by environmental, genetic and ontogenetic mechanisms including phenotypic plasticity, ecological filtering, adaptive evolution, or tree age (Aitken et al., 2008; Messier et al., 2017). Using a variance-based approach focused on individuals may provide insights into the mechanisms by which functional traits modulate the ability of a tree to persist and reproduce in the face of rapid shifts in environmental conditions (Violle et al., 2012).

Intraspecific variability in certain functional traits (i.e., drought response traits *sensu* Anderegg and HilleRisLambers, 2016) may enhance tree species' acclimation potential to drought and will potentially afford resilience in an increasingly unpredictable environment (Nicotra et al., 2010; Anderegg, 2015). For example, phenotypic plasticity associated to changes in interannual environmental conditions can define the capacity of trees to adjust quickly enough before death to increasingly frequent severe droughts (Ramírez-Valiente et al., 2015). Previous studies evaluating ITV across environmental gradients (e.g., Martí- nez-Vilalta et al., 2009; Rosas et al., 2019; Anderegg et al., 2021) and its association with tree responses to drought (González de Andrés et al., 2021) were conducted at single time points. Therefore, this snapshot approach disregards temporal variability caused by developmental timing or variations in weather conditions over time (Cope et al., 2022), which has been proven significant in functional traits across different years (García-Cervigón et al., 2020; Kerr et al., 2022; Vasey et al., 2022) and within years (Fajardo and Siefert, 2016; Bloomfield et al., 2018). Year-to-year phenotypic plasticity has been previously analyzed in common garden experiments, but this approach prevents studying mature stands. To address this limitation, temporal variation of traits on the same individuals needs to be measured as has been done with xylem traits following retrospective tree-ring approaches (Borghetti et al., 2017).

Different traits are expected to reflect tree performance along environmental gradients. Morphological and structural traits are easily measured and can be tractable assessed across hundreds or thousands of individuals. Although these traits entail drought-related and non-drought-related anatomical traits, adjustments along water availability gradients have been found. Reduction of leaf area decreases surface of transpiration in dry atmospheres and improve convective cooling (Gil-Pelegrín et al., 2017). Hence, increased leaf mass per area (LMA) is associated with drought-prone environments (Wright et al., 2004). High LMA improves water use-efficiency by reducing epidermal water loss and enhancing hydraulic function but at the expense of less productive leaves (Poorter et al., 2009). Furthermore, changes in allocation patterns and productivity between leaves (light interception and hydraulic demand) and sapwood (hydraulic supply) may also reflect drought avoidance strategies. For instance, high sapwood to leaf area ratios are positively related to aridity due to lower evaporative demand and reduced xylem tension for water transport (Martínez-Vilalta et al., 2009). However, such reports have been conducted across spatial gradients in environmental conditions and, to our knowledge, there is no study evaluating the adjustment of these traits across years in adult trees among different populations under contrasting climatic conditions.

Tree radial growth is considered a sensitive indicator of tree carbon-water balance and it is largely driven by environmental conditions (Babst et al., 2018). Therefore, examining the variance patterns of tree rings and their covariation with functional traits can improve our understanding of tree fitness under changing conditions. Different scale-dependent drivers shape trait and growth variability across ecological scales (Albert et al., 2010; Messier et al., 2010). Additionally, morphological traits and productivity measurements are key parameters in vegetation models that contribute advancing our current knowledge

of climate change impacts on forest ecosystems (van Bodegom et al., 2014).

In this study, we focused on two groups of coexisting Mediterranean oak species with contrasting foliar habits: evergreen oaks (*Quercus ilex* ssp. *ilex* L. and *Q. ilex* ssp. *ballota* (Desf.) Samp.) and deciduous oaks (*Quercus faginea* Lam. and *Quercus humilis* Mill.). The functional strategies of these taxa are shaped by the contrasting climatic environments they inhabit (hot and dry summers and cold winters across inland regions) and their high phenotypic variability (Montserrat-Martí et al., 2009). Assessing the variation in functional traits and drought performance of these taxa with contrasting foliar habits but growing under the same environmental conditions may improve our understanding of the different strategies they adopt to cope with water deficit. Studies evaluating variability in traits related to leaf structural and chemical composition, xylem and root traits (Castro-Díez et al., 1997; Villar-Salvador et al., 1997; Coll et al., 2012), trait coordination (Rosas et al., 2019; Ramírez-Valiente et al., 2020), drought performance and tolerance strategies (Corcuera et al., 2004a,b; Gutiérrez et al., 2011) have been conducted in Iberian oaks. However, the assessment of patterns of ITV across different ecological scales and along environmental gradients, and their covariation with tree performance using a long-term approach has not yet been attempted.

Here, we examine the extent of spatial and temporal intraspecific variation in morphological and structural traits (ITV) and radial growth of the evergreen *Q. ilex* and the deciduous *Q. faginea* and *Q. humilis* Mediterranean oaks. It should be noted that the term ITV in this study refers to the variation within each foliar habit group comprising closely related taxa. Our dataset was collected along a wide water availability gradient in northeastern Spain over a six-year period, during which the same trees were recurrently sampled. This comprehensive dataset enabled us to fulfill the following objectives: (1) to investigate trait variability across different ecological scales; (2) to characterize trait-by-drought relationships and the ITV along water availability gradients; and (3) to assess the relation between ITV and tree growth responses to drought. We hypothesize that (1) within-crown (among-branch) and year-to-year variation in trait values, which is a measure of phenotypic plasticity, will represent a non-negligible part of intraspecific variation for both, evergreen and deciduous oaks; (2) ITV will be constrained under drier conditions and in arid sites reflecting both impaired performance during drought and stronger environmental filtering; and (3) tighter covariation between growth and trait variation will be expected at broader spatial scales (i.e., among sites) reflecting greater gradient differences than microsite limitations.

2. Materials and methods

2.1. Study area and study species

We selected six sites in northeastern Spain where evergreen and deciduous Mediterranean oaks coexist (Fig. 1a). Study sites were distributed along a coast-inland gradient with contrasting climatic conditions. Coastal sites were Orduña (OR) and Collserola (CO) and they received Atlantic and Mediterranean influences, respectively. OR presents by far the highest annual precipitation, particularly from winter to spring, whereas dry summers and wet autumns characterize CO. Soria (SO), Oliola (OL) and Alcubierre (AL) sites have continental conditions with large contrasts between maximum and minimum temperatures and relatively low precipitations. AL is a semi-arid site showing the lowest precipitation, whereas SO is the coldest site. Finally, intermediate climate conditions between coastal and inner sites can be found in Sansoáin (SA) (Fig. 1b).

Climate data were obtained from the 0.1º gridded E-OBS 27.0e database (Cornes et al., 2018). During the 2008–2013 period, the mean annual temperatures ranged from 9.5 (SO) to 16.4 ºC (CO), and annual precipitation was found to be between 401 (AL) and 841 mm (OR) (Table S1). July and August were the warmest and driest months, while
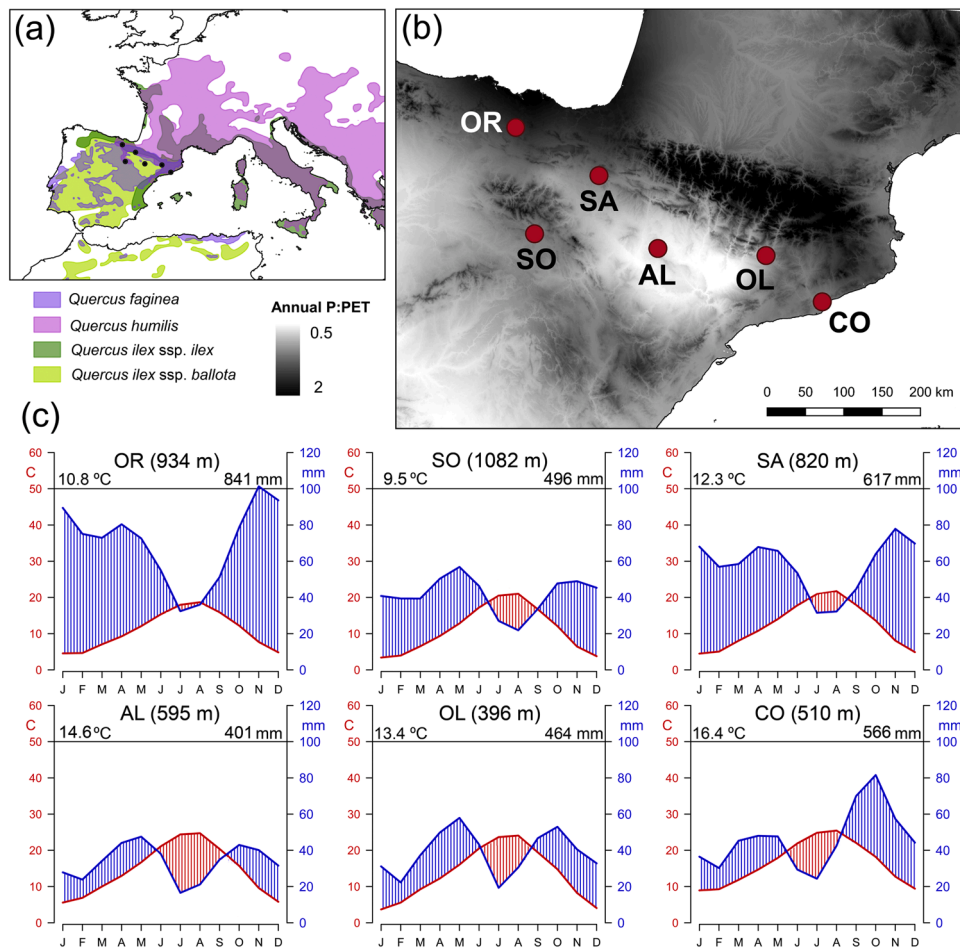
Fig. 1. (a) Distribution range of *Quercus ilex* ssp. *ilex* (dark green area), *Q. ilex* ssp. *ballota* (light green area), *Q. faginea* (purple area) and *Q. humilis* (pink area) (de Rigo et al., 2016), and location of study sites in southern Europe (black dots). (b) Geographic position of study sites in northeastern Spain. The grey-scale background map represents spatial variation of the ratio between precipitation and potential evapotranspiration (P:PET) (climate data from Fréjaville and Benito Garzón, 2018). (c) Climatic diagrams for each study site according to climatic data retrieved from E- OBS v. 27.0e database (Cornes et al., 2018) for the period 2008 – 2013.

precipitation peaked in spring and autumn depending on the site (Fig. 1c). To characterize aridity conditions, we calculated the annual ratio of precipitation and potential evapotranspiration averaged for the period 1980–2017 (site P:PET) according to the Thornthwaite equation (1948). Furthermore, we also obtained data of the Standard Precipitation and Evapotranspiration Index (SPEI) at a spatial resolution of 1.1-km (Vicente-Serrano et al., 2017) for each studied site. The SPEI is a standardized multi-scalar drought index based on the accumulated water deficit, in which negative and positive values indicate relatively dry and wet conditions, respectively (Vicente-Serrano et al., 2010).

We studied two functional groups of Mediterranean oaks according to their foliar habit. The combination of the closely related taxa included in each group is supported by their degree of hybridization. The evergreen group was represented by *Q. ilex*, which is distributed across the western Mediterranean basin (Fig. 1a). *Q. ilex* is a diffuse to semi-ring porous species that presents large morphological variation in foliar traits resulting in different morphotypes going from long lanceolate to short, rounded leaves (Peguero-Pina et al., 2014; Niinemets, 2015). In the two coastal sites (CO and OR) *Q. ilex* individuals belong to the subsp. *ilex*, whereas in the inland sites the morphological traits correspond to the subsp. *rotundifolia*. The two subspecies do not co-occur in any site simultaneously. The winter deciduous group of Mediterranean oaks consists of the ring porous species *Q. faginea* and *Q. humilis*. The former is distributed across the Iberian Peninsula and north of Africa, while the latter is widely distributed across central and southern Europe (Fig. 1a). Both species form an ecological continuum and they commonly hybridize in the northeast of Iberian Peninsula, but only individuals clearly identified as belonging to one or another species at each site were selected. The leaf and acorn characteristics corresponded to *Q. faginea* in all sites except the coastal Mediterranean site CO, where traits corresponded clearly to *Q. humilis*. All study sites corresponded to secondary forests where most trees were relatively young (30–70 years), and had colonized former croplands and grasslands.

2.2. Field sampling and traits measurements

In 2008, six 0.5 ha plots were established in the study sites where healthy-looking mature trees were selected. In each plot, ten *Q. ilex* and *Q. faginea* individuals (OR, SO, SA, AL and OL) and fifteen *Q. ilex* and *Q. humilis* individuals (CO) were tagged and their diameter at breast height (DBH) measured. In total, 130 trees were sampled (65 *Q. ilex* ssp. *ilex*/ *Q. ilex* ssp. *ballota* and 65 *Q. faginea*/*Q. humilis*) across the study region. During a 6-year period (2008–2013), two branches (one sun-exposed branch and one shaded branch) 50–140 cm long were randomly sampled from the upper canopy of each individual to characterize leaf and shoot traits. This sampling was designed to capture the widest possible range of variability within the crown. Collected branched accounted for a small proportion on the crown removed each year, so we assume that tree performance was not affected. Sampling was conducted on the date when primary growth had finished and leaf shedding of deciduous species had not yet begun (Table S2) in order to capture comparable phenological stages across sites. Measurements

were repeated on the same individuals each year to minimize the effect of genotypic and site differences.

Trait measurements were conducted following standard protocols (Pérez-Harguindeguy et al., 2013). Collected branches were transported to the laboratory and two to five current-year shoots per branch were randomly selected. The leaf area of every leaf produced by each shoot in that year were scanned and their summed area measured with ImageJ software (Schneider et al., 2012) while being still fresh. Afterwards, twig and leaves produced by each shoot were oven-dried during 48 h at 60 ºC and weighted to 0.01 g precision. The following variables were derived: the area of all the leaves produced by a shoot (LA), the dry weight of a shoot twig (Sm), the leaf mass per area of all the leaves produced in a shoot (LMA), and the ratio of shoot twig to leaf biomass (Sm:Lm). LA and Sm reflect the growth and carbon allocation in primary growth and how it is distributed in different shoot parts. LMA is a structural trait, which relates to other chemical and structural leaf traits within the leaf economics spectrum (Wright et al., 2004). The ratio Sm:Lm is an indicator of carbon allocation patterns between shoots and leaves. These measures were repeated every year except for 2008 at CO site. Across the six years, we measured 3144 shoots and 21,954 leaves of *Q. ilex* and 3061 shoots and 17,043 leaves for *Q. faginea* and *Q. humilis*.

2.3. Dendrochronological methods

Radial growth of selected trees was evaluated using dendrochronology. In summer 2017, one or two cores per tree were extracted at 1.3 m height using 5 mm Pressler increment borers (Haglöf, Sweden). The wood samples were processed following standard dendrochronological methodologies (Fritts, 2001). All cores were visually cross-dated and ring widths were measured to a precision of 0.001 mm using a LINTAB measuring device (Frank Rinn). The visual cross-dating was statistically checked using the COFECHA software (Holmes, 1983). Descriptive statistics of tree ring data were calculated (Table S2). Tree-ring width series were transformed to basal area increment (BAI) series to account for geometrical constraints (Biondi and Qeadan, 2008). BAI was calculated assuming a circular shape of stems and using the formula:

$$BAI = \pi\left(R^2_t - R^2_{t-1}\right) \tag{1}$$

where R^2_t and R^2_{t-1} are the radius of the tree in the year of growth (*t*) and the previous year (*t*-1). To carry out the following analyses, we used BAI values for each year in the period 2008–2013. Tree ring series processing and dendrochronological statistics calculation were performed using the package *dplR* (Bunn et al., 2020) from the R software (R core Team, 2022).

The study period encompassed the severe drought event occurred in 2012, which impaired forest productivity and triggered forest dieback episodes in northeastern Spain (Camarero et al., 2015; J.J. 2016). This provided an opportunity to study the growth response to an extreme climatic event and its relationship to morphological traits. We calculated the resilience indices proposed by Lloret et al. (2011) based on the ratios of pre- drought (BAI$_{preD}$), drought (BAI$_D$) and post- drought (BAI$_{postD}$) radial growth values as follows:

$$Resistance = BAI_D / BAI_{preD} \tag{2}$$

$$Recovery = BAI_{postD} / BAI_D \tag{3}$$

$$Resilience = BAI_{postD} / BAI_{preD} \tag{4}$$

We used windows of three years before and after drought occurrence to calculate tree-level resilience indices.

2.4. Statistical analysis

Variance of traits – Total trait variation within each foliar habit was evaluated using the coefficient of variation (CV). To understand the distribution of variability across different ecological scales, we carried out a variance partitioning analysis following Messier et al. (2017, 2010). Intercept only linear mixed-effects models (LMMs; Pinheiro and Bates, 2000) were fitted for each trait and foliar habit using branch-level trait data that included a random effect structure in which tree nested within site which in turn is nested within taxon are crossed with year: [(1|Taxon/Site/Tree) + (1|Year)]. This model is biologically realistic because it allows years to occur in multiple taxa, sites and trees. In the tree-level radial growth models, random effects were included as: [(1| Taxon/Site) + (1|Year)]. The resulting variance estimate for taxon represents variation among subspecies (evergreen oaks) or species (deciduous oaks), the variance estimate for tree and site represents variation within- and among-populations, respectively, and the variance estimate for year along with the residual variance represents within-crown variation plus measurement error, which is jointly interpreted as phenotypic plasticity.

We also calculated the $T_{IC/IR}$ statistic proposed by Violle et al. (2012) to analyze population-level trait variance by taking each site as a different population. This index represents traits' values dispersion in each population (*IC*) in relation to the observed variance across the whole spatiotemporal gradient of the species (*IR*) and it quantifies the strength of environmental filtering (e.g., climatic constraints) in traits' expression (Violle et al., 2012). The closer the $T_{IC/IR}$ value to 0 (i.e., less scattered trait in relation to the regional pool), the stronger the external filtering on the population. To separate the spatial and temporal components of $T_{IC/IR}$, we averaged mean trait values across years and across trees to calculate spatial $T_{IC/IR}$ (among-trees) and temporal $T_{IC/IR}$ (among-years), respectively. To be included in further analysis, spatial $T_{IC/IR}$ was determined for each year separately and temporal $T_{IC/IR}$ values were assigned to each tree within a site. $T_{IC/IR}$ values were calculated using the R-package *cati* (Taudiere and Violle, 2016).

Effect of water availability on trait adjustments and variances – We used LMMs to evaluate trait-by-water availability relationships. For each foliar habit, branch-level trait data were fitted against the drought index (SPEI) and site P:PET. We also included DBH and tree age as individual level covariates. To identify seasonality of SPEI (i.e., time scale and month) that better explained the observed patterns of each trait, we fitted separated models of trait values against 1-, 3-, 6-, 9- and 12-month SPEI values for every month of the year, we ranked all potential models according to Akaike Information Criterion (AIC; Burnham and Anderson, 2002) and selected the model with the lowest AIC value. A random intercept associated with tree nested within site nested within taxon and crossed with year was included as explained above.

To examine the effect of drought on trait variance, above branch-level trait-by-water availability LMMs were fitted including different variance structures that represent the change of variance as exponential or potential functions of previously selected SPEI and site P:PET (Table S3). We determined if models including nonconstant variance functions improved fixed variance models using the likelihood ratio test. In addition, we fitted LMMs of temporal and spatial $T_{IC/IR}$ against selected SPEI and site P:PET. Site nested within taxon was regarded as a random factor since multiple measures (different trees or years) occurred at each site and taxon.

Covariation between traits and radial growth – We evaluated the relationship of leaf and shoot traits with BAI and drought response indices. Firstly, LMMs between BAI and mean values of traits during the study period 2008–2013 were fitted for each trait and foliar habit. To test if the covariation between BAI and traits depended on drought stress, we included SPEI and its interaction with trait. Models were fitted at tree- and site-levels to evaluate if trait impact on BAI changed at different ecological scales. To test if populations showing higher ITV grew more, site-level models also included spatial $T_{IC/IR}$ and its interaction with SPEI as covariates. Secondly, tree-level drought resilience indices were fitted against mean tree trait values. We also included temporal $T_{IC/IR}$ as fixed effects to check whether trees with greater phenotypic plasticity performed better in the face of the 2012 drought. Tree- and site level models

included a random intercept of tree nested within site nested within taxon and site identity, respectively.

All values of leaf and shoot traits and growth (BAI) were log-transformed before analysis to meet assumptions of normality. Variables were standardized by subtracting the mean and dividing by the standard deviation prior to the LMM analyses to obtain comparable parameters across covariates. All analyses were performed in the R statistical environment (R core Team, 2022). LMMs were fitted using the *lme4* and *lmerTest* packages (Bates et al., 2015; Kuznetsova et al., 2017) for fixed variance models, or the *nlme* package for more complicated variance structures (Pinheiro et al., 2020). In the latter case, the effect of year in the structure of data was included as a first-order autocorrelation structure.

3. Results

3.1. Variance of traits

The most variable trait at the intraspecific level was shoot twig mass (Sm; CV *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* = 19.1 %, *Q. faginea/Q. humilis* = 20.9 %), followed by Sm:Lm (CV *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* = 11.6 %, *Q. faginea/Q. humilis* = 11.8 %), whereas leaf-related traits (leaf area and leaf mass per area) showed the least variation (LA: CV *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* = 9.1 %, *Q. faginea/Q. humilis* = 9.0 %; LMA: *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* = 7.2 %; *Q. faginea/Q. humilis* = 8.3 %) (Fig. S1). In both species, variance decomposition showed the largest ITV at lower ecological scales (within trees for morphological traits and within populations for BAI). This phenotypic plasticity accounted for over half of the total variance in most traits except for LMA and LA in evergreen and deciduous oaks, respectively (Fig. 2a). Variation associated to different species within each foliar habit was negligible for most of traits excluding LMA in evergreen oaks *(Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota)* and primary growth (LA and Sm) in deciduous oaks *(Q. faginea/Q. humilis)*. Variation among trees within a site was smaller than variation among sites.

Population-level variance ($T_{IC/IR}$) differed between traits and foliar habits (Table 1). LMA and LA showed the lowest $T_{IC/IR}$ means in evergreen and deciduous oaks, respectively, thus highlighting the strongest environmental filtering on those traits. At the other end we found Sm:Lm with the highest $T_{IC/IR}$ in both foliar habits. The ratio between temporal and spatial $T_{IC/IR}$ was close to one for LA, Sm and Sm:Lm; that is, those

Table 1
Morphological traits and radial growth during 2008–2013 period for the study Mediterranean oaks. For each trait, mean values (standard errors) and population-level trait variance ($T_{IC/IR}$, where IC and IR are the variances of population and of the species, respectively, for a given trait T; Violle et al., 2012) are presented.

	Evergreen		Deciduous	
	Mean (SE)	$T_{IC/IR}$ (SE)	Mean (SE)	$T_{IC/IR}$ (SE)
Leaf area (LA, cm^2)	18.01 (0.22) a	0.85 (0.10)	35.51 (0.55) b	0.58 (0.05)
Shoot twig mass (Sm, mg)	92.59 (1.56) a	0.84 (0.04)	109.87 (2.44) a	0.69 (0.08)
Leaf mass per area (LMA, mg cm^{-2})	20.99 (0.08) a	0.49 (0.08)	12.46 (0.05) b	0.71 (0.14)
Sm:Lm	2.59 10^{-1} (2.99 10^{-3}) a	0.97 (0.07)	2.53 10^{-1} (3.27 10^{-3}) b	0.91 (0.17)
Basal area increment (BAI, cm^2 y^{-1})	4.83 (0.20) a	0.71 (0.09)	4.35 (0.17) b	0.87 (0.15)

Different letters indicate significant differences ($p < 0.05$) in mean values between evergreen and deciduous oaks according to the Kruskal Wallis test.

traits shared similar proportion of variation across years and sites. LMA and BAI spatial variances were greater than temporal variance (Fig. 2b).

3.2. Effect of water availability on trait adjustments and variances

Both groups of Mediterranean oaks showed a consistent response of greater productivity (increased LA, Sm and BAI) and lower LMA with increasing water availability. SPEI had a significant effect in all traits of both foliar habits, whereas site P:PET only influenced LA of *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* and Sm, LMA and Sm:Lm of *Q. faginea/Q. humilis* (Table 2). Thus, seasonal climatic conditions characteristic for each trait and species arose as more important drivers of trait adjustments than mean aridity conditions. Primary growth traits (LA and Sm) and LMA positively and negatively responded, respectively, to increasing short-term water availability during spring (Fig. 3a-c). Deciduous species showed trait response to earlier conditions (March (LA) and April (LMA)) compared to the evergreen species (April and May). The impact of drought conditions on Sm:Lm and radial growth (BAI) occurred at longer time scales (six to nine months) and differed between foliar habits (Fig. 3d and e). Previous winter and spring conditions had a positive
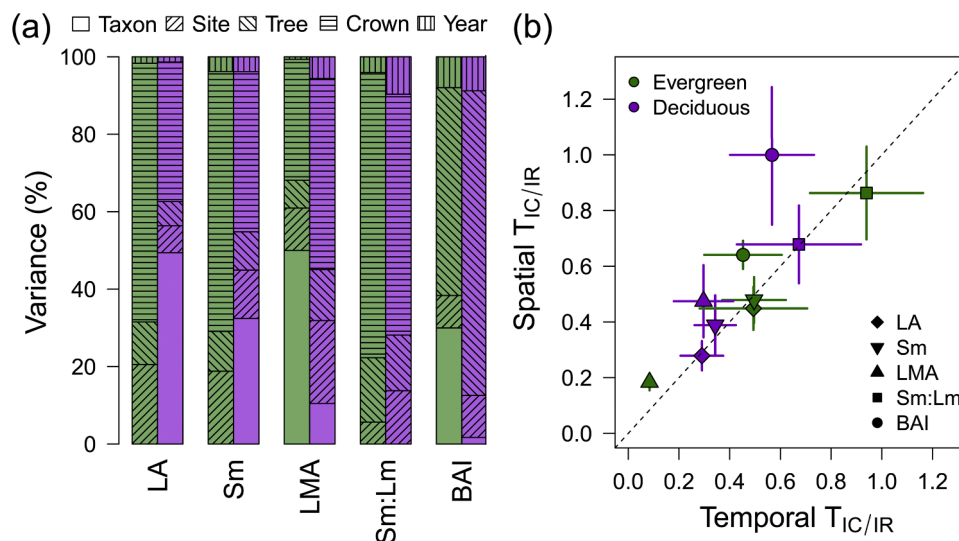
Fig. 2. Variance partitioning across different levels of organization (a); relationship between temporal and spatial population-level variance ($T_{IC/IR}$ statistic, Violle et al., 2012). Error bars indicate standard errors among sites (b). Abbreviations for traits are: leaf area (LA), shoot twig mass (Sm), leaf mass per area (LMA), the ratio of shoot twig mass by leaf mass (Sm:Lm), and basal area increment (BAI). Green and purple bars in (a) and points in (b) represent evergreen and deciduous oaks, respectively.

Table 2
Linear mixed-effects models characterizing the trait-by-water balance relationships. Selected time scale and month of the SPEI are indicated. Standardized coefficients (lower/upper confidence limits) and significance level (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) are shown only for significant fixed effects. Abbreviations of traits are listed in Table 1. Note that seasonality of SPEI is indicated as follows: the first digit refers to the time scale in months and the abbreviation of the month indicates the last month considered in its calculation.

Group	Trait	SPEI		Site P:PET	DBH	Tree age
Evergreen	LA	1.Apr	0.32 (0.25/0.37)***	0.31 (0.06/0.68)*		
	Sm	3.May	0.14 (0.09/0.20)***			
	LMA	1.Apr	−0.03 (−0.04/−0.01)***			
	Sm:Lm	9.Aug	0.09 (0.06/0.13)***			
	BAI	9.Aug	0.20 (0.12/0.29)***		0.27 (0.22/0.38)***	−0.16 (−0.26/−0.06)**
Deciduous	LA	1.Mar	0.04 (0.01/0.07)*			
	Sm	1.Mar	0.15 (0.10/0.20)***	0.26 (0.05/0.48)*		
	LMA	1.Apr	−0.04 (−0.06/−0.03)***	−0.08 (−0.13/−0.02)*		
	Sm:Lm	6.May	0.04 (0.01/0.06)*	0.16 (0.06/0.25)***		
	BAI	6.May	0.14 (0.04/0.24)**		0.29 (0.21/0.36)***	−0.17 (−0.24/−0.09)**

effect on Sm:Lm and BAI of deciduous species, whereas the effect extended to summer in the case of the evergreen species. Tree DBH and age were only significant covariates in BAI models and they had positive and negative effects on radial growth, respectively (Table 2).

We found stronger evidence for increasingly constrained branch-level trait variation under drier conditions in the deciduous than in the evergreen oaks (Table 3). On one hand, trait-by-water availability model of LMA for the evergreen *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* improved when variance was allowed to change along SPEI gradients. In contrast, Sm variance decreased along gradients in spring water availability. On the other hand, variance structures of LMMs fitting LA, Sm and Sm:Lm of the deciduous *Q. faginea/Q. humilis* supported decreasing variance as site P:PET decreased. For both foliar habits, the greater the water shortage during their growing season, the greater the BAI variability. Our results also support constrained population-level trait variance by water availability with this effect being stronger in deciduous species (Table S4). For these species, spatial $T_{IC/IR}$ and temporal $T_{IC/IR}$ of LA, Sm and Sm:Lm were constrained as site P:PET or seasonal SPEI decreased, respectively (Fig. 4). In evergreen oaks, only temporal $LA_{IC/IR}$ positively responded to increasing water availability.

3.3. Covariation between traits and radial growth

At the tree-level, we found a negative relationship between BAI and LMA in *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* and positive between BAI and Sm and Sm:Lm in *Q. faginea/Q. humilis* (Table 4). Trait-BAI covariation in deciduous oaks was maintained between tree- and site-levels. However, positive significant relationships of LA, Sm and Sm:Lm with BAI emerged in the evergreen species when moving to population scales (Fig. 5a–c). It should be noted that at the site-level the association of BAI with LMA was not related to mean values but rather to $LMA_{IC/IR}$ (Fig. 5d). $LA_{IC/IR}$ was also positively linked to BAI of the evergreen oak (Fig. 5e). Therefore, the greater the variance of LA and LMA among trees within a site, the greater the mean BAI of the population. Trait covariation was mediated by drought conditions only in the deciduous group. The negative interaction between Sm and Sm:Lm with SPEI6.May indicated that covariation strength decreases as water availability increases (Table 3).

None of the resilience indices against the 2012 drought of evergreen oaks showed a significant relationship with mean or variance trait values. In contrast, we found significant relationships between resistance and resilience of deciduous oak species and temporal $T_{IC/IR}$ of LA, Sm and Sm:Lm (Table S5; Fig. 6). These results suggest that the short-term drought response of deciduous oak trees is enhanced by higher phenotypic plasticity in leaf and shoot traits. It is worth noting that while there are trees with reduced trait plasticity that show diverse responses to drought, trees with high phenotypic plasticity are consistently more resistant and resilient to the 2012 drought (Fig. 6).

4. Discussion

4.1. Ecological scale of trait variation

Ecologists and tree physiologists have long been interested in leaf trait variability of Mediterranean oaks. In this study the highest portion in trait variation was detected at the lowest ecological scale, within individual trees (Fig. 2a). Variation at sub-individual levels has not received much attention, albeit the potential importance that it could exert on ecological processes (Herrera, 2017). It might reflect differences in age, micro-environmental conditions or disturbance history (Albert et al., 2010; Funk et al., 2017). For example, relative leaf position within the tree crown causes different microenvironmental conditions (e.g., light, temperature and water stress) that led to trait differences in Mediterranean oaks (Rubio de Casas et al., 2007; Mendiavilla et al., 2019). Changing environmental (climatic) conditions can also drive year-to-year variation of traits within trees. In this dataset, such variation represents a small proportion of the total variance. While both sources of variation (i.e. crown position and year) can be confused due to the sampling of different branches each year, they occur at the sub-individual level and can thus be interpreted as phenotypic plasticity (Nicotra et al., 2010). Phenotypic plasticity accounts for more than half of variation in most of the traits for both, deicuduous and evergreen oaks, thus supporting our first hypothesis. This is relevant as phenotypic plasticity has been proposed to be the major means by which plants cope with environmental heterogeneity (Valladares et al., 2007). At the population-level, spatial and temporal trait variance ($T_{IC/IR}$) become comparable (Fig. 2b) suggesting a similar significance in the variation of environmental conditions among sites and across years that drive trait adjustments (Dwyer et al., 2014).

Genetic differences between species drive considerable variation in specific traits of each foliar habit: LMA of the evergreen oaks and primary growth (LA and Sm) of deciduous oaks (Fig. 2a). Considering the different distribution of the subspecies and species (Fig. 1a), these results can support genetic adaptive modifications in response to long-term site climate. It is reasonable to expect that an evergreen and sclerophyllous species such as *Q. ilex* would cope with variable water availability through modifications in LMA, while the deciduous *Q. faginea* and *Q. humilis*, which are more mesic species, would use LA adjustments for the same purpose. Trait variation across sites was generally higher than among individuals of a given site (Fig. 2a), indicating that macroclimatic patterns are stronger drivers of ITV than within site differences in evergreen and deciduous Mediterranean oaks and across their distribution area in northeastern Spain. It is important to note that when we refer to ITV, we mean the variation within each foliar habit conformed by closely related taxa. Broad-scale patterns in variance structures hint indirect evidence of populations local adaptation allowing species distribution to track directional climate change by
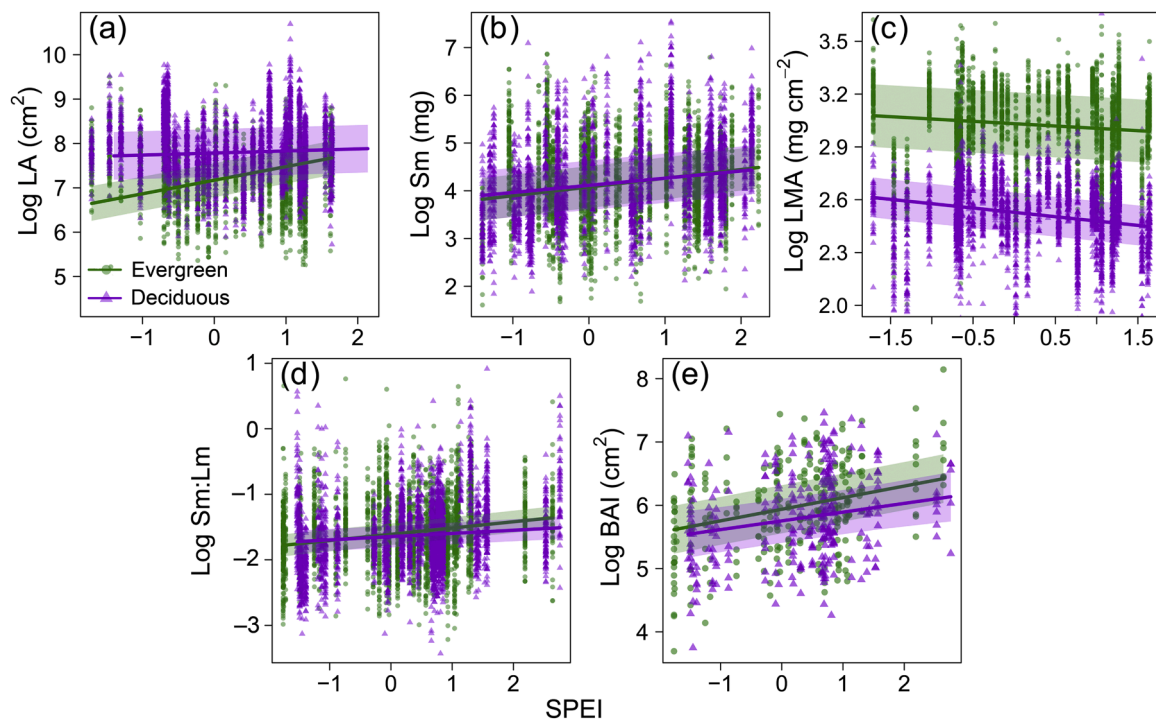
Fig. 3. Relationships between leaf, shoot and BAI and Standard Precipitation and Evapotranspiration Index (SPEI). Month and time scales of SPEI for each trait and species can be found in Table 2. Solid lines represent significant effects according to LMMs and shaded areas represent 95 % confidence intervals (Table 2). Green and purple symbols and lines represent evergreen and deciduous oaks, respectively.

Table 3

Variance structure of the selected models characterizing the trait-by-drought relationships. The table shows the climatic covariate estimate introduced as power (p) or exponential (e) functions and the χ^2 statistic and the associate *p*-value of the Likelihood Ratio Test comparing to fixed variance models.

|	Evergreen			Deciduous		
	Covariate	Estimate	χ^2	Covariate	Estimate	χ^2
LA				Site P:PET	0.219 (p)	17.641***
Sm	SPEI3.May	−0.043 (e)	6.371*	Site P:PET	0.313 (p)	33.574***
LMA	SPEI1.Apr	0.084 (e)	24.462***			
Sm:Lm				Site P:PET	0.643 (e)	106.84***
BAI	SPEI9.Aug	−0.124 (e)	6.328*	SPEI6.May	−0.161 (e)	9.828**

providing pre-adapted propagules (Jump and Peñuelas, 2005; Albert et al., 2011). Camarero et al. (2012) found constitutive differences in foliar traits of *Q. ilex* in three of our study populations. Thus, our results also highlight the major role of genotypic differences among populations in shaping spatial trait variation considering their different provenances (Table S6) (Alía et al., 2009). However, the contribution of plastic adjustments to the environment and their interaction with genotype cannot be rejected (Albert et al., 2010).

4.2. Trait adjustments and variances along water availability gradients

We found a consistent trait response within both evergreen and deciduous Mediterranean oaks across a wide spatiotemporal drought gradient (Fig. 3), thus highlighting the relevance of climate variability in driving trait shifts over space and time (Bloomfield et al., 2018; Kerr et al., 2022). As environment gets drier, trees shift from acquisitive to conservative water-use strategies (Reich, 2014). Leaf morphological modifications have been proposed as key strategies that allow Mediterranean oaks to withstand water deficit by improving water use efficiency (Peguero-Pina et al., 2014; J.J. 2016). Our results are in line with previous studies on these species that also reported reduced LA and increased LMA as conditions became drier (Niinemets, 2015; Ramírez-Valiente et al., 2020; Salazar Zarzosa et al., 2021; Solé-Medina et al.,

2022). Growth of woody tissues showed strong positive response to water supply consistent with their high climate sensitivity due to the preferential allocation to photosynthetic tissues under resource limitation (Kannenberg et al., 2019), which is also supported by the positive SPEI – Sm:Lm association. This result is somewhat inconsistent with the well-established positive relationship between aridity and sapwood-to-leaf area ratio (Rosas et al., 2019; López et al., 2021). At the whole plant level, the Sm:Lm ratio was found to decrease with increasing annual temperature with no effect of aridity (Reich et al., 2014; Durrsma and Falser, 2016). This effect could be mediated by tree height, as both variables have been reported to covary positively (Durrsma and Falser, 2016). However, we found no effect of tree size on Sm:Lm (Table 2), preventing us from drawing clear conclusions about its underlying climatic drivers.

An interesting outcome of the present study is the seasonality patterns of drought in the trait-by-water availability relationships since seasonal variation in abiotic properties drives a significant proportion of ITV (Moore et al., 2020; Westerband et al., 2021; Schmitt et al., 2022). Specific trait and species responses are in accordance with their phenology. Most of the shoot development occurs during spring in both species, although the deciduous oaks sprout and start leaf development at least two weeks before the evergreen oak (Table S2) (Montserrat-Martí et al., 2009). Likewise, tree ring formation peaks in spring
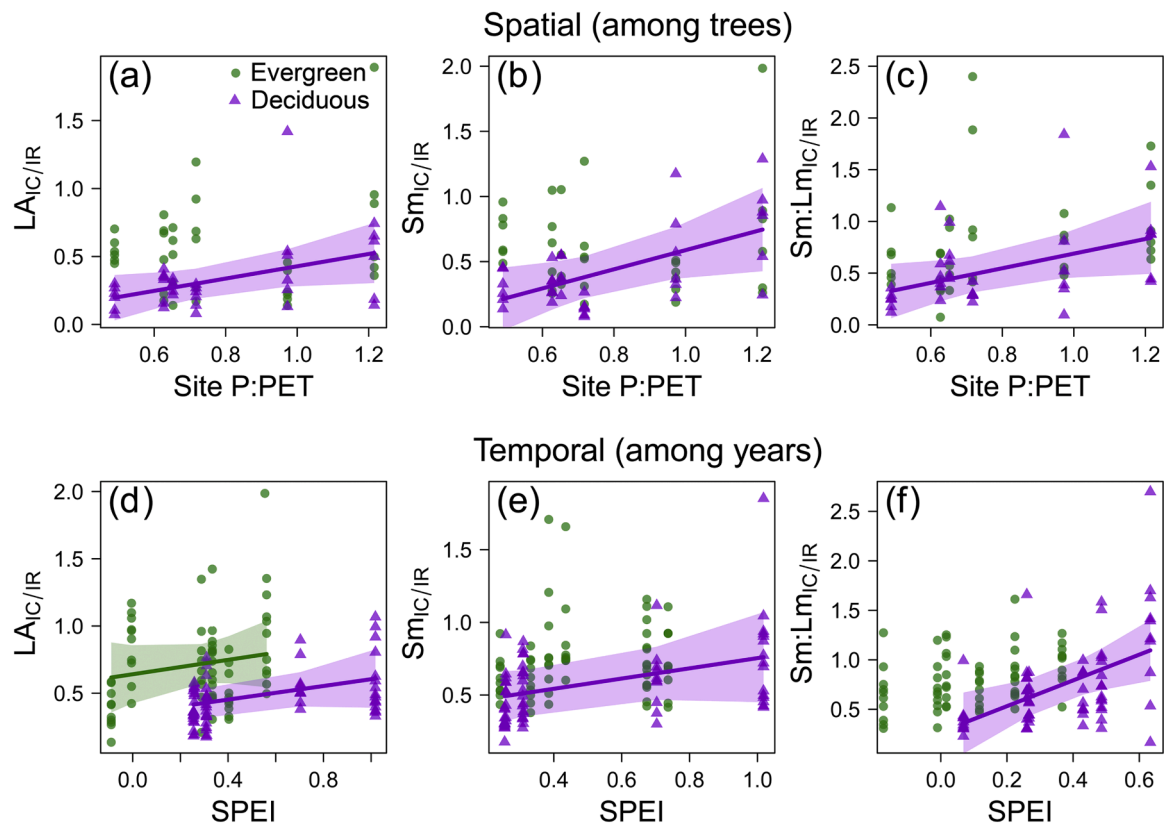
Fig. 4. Relationship between population-level variances ($T_{IC/IR}$) and water availability, among-trees (a-c) and among-years (d-f). Water availability variables were mean annual P:PET for each site during 1980–2017 (site P:PET) and Standard Precipitation and Evapotranspiration Index (SPEI). Time scale and month of SPEI for each trait are the same as in Table 2. Solid lines represent significant effects according to linear mixed-effects models (see Table S4) and shaded areas are 95 % confidence intervals. Green and purple symbols and lines represent evergreen and deciduous oaks, respectively.

across species, but only *Q. ilex* maintains some growth during summer and displays stronger autumn growth peak due to its facultative bimodality (Tumajer et al., 2022). These differences result from contrasting strategies adopted by each species to cope with summer drought. High cavitation risks associated with large earlywood vessels of the ring porous deciduous species led to a drought avoidance strategy through sharp decreases in photosynthetic activity and advanced leaf shedding (J.J. Camarero et al., 2016; Resco de Dios et al., 2020). In contrast, the smaller vessels of *Q. ilex* increase xylem cavitation resistance, making it more drought-tolerant (Corcuera et al., 2004b; Montserrat-Martí et al., 2009).

Understanding how trait variances change along water climatic gradients may be more relevant to forecast plant responses to climate change than trait means (Anderegg et al., 2021). We observed two contrasting patterns of variance in response to water availability between traits and radial growth. On one side, and according to our second hypothesis, variances of leaf and shoot traits are constrained by water deficit (Table 3, Fig. 4). These outcomes support previous studies reporting reduced trait variance as climatic conditions become harsher, i.e., climatic filtering (Ramírez-Valiente and Cavender-Bares, 2017; Anderegg et al., 2021; Stotz et al., 2021; Vicente et al., 2022). For instance, Anderegg et al. (2021) found that within-species variance of leaf dry mass content was increasingly limited at higher arid conditions. Likewise, Vicente et al. (2022) observed that aridity reduced variance of traits related to the maintenance of water status in beech trees. Constraints of trait variance differed between foliar habits. We found stronger evidence of variance limitation by drought in the deciduous oaks as more traits were affected across different ecological scales. This finding is consistent with the higher drought sensitivity of these species, and it agrees with the lower multivariate plasticity displayed in *Q. faginea* populations from harsher (drier and colder) environments

found by Solé-Medina et al. (2022). High ITV can be advantageous for coping with highly variable conditions (Anderegg, 2015), but it also implies excessive costs in low-resource environments (Valladares et al., 2007). Thus, our results support the tradeoff between increased stress tolerance and the ability to cope with highly variable conditions through increased trait variation (Power et al., 2019), particularly for *Q. faginea/ Q. humilis*. Conservative resource-use imposed by arid conditions can, therefore, reduce trait variation and select trait values that promote maintenance of tree water balance. Such mechanisms seem to operate on different traits for each oak group; namely, on LMA for evergreen species and on primary growth (LA, Sm and Sm:Lm) for deciduous species. This is consistent with the idea that trait variation is species-specific, and traits vary independently despite being related (López et al., 2021). Moreover, the same traits showed the strongest climatic filtering, highlighting their relevant role in coping with drought in each species group.

On the other side, variance of radial growth increased when water availability during the growing season decreased (Table 3), in agreement with previous studies (Andreu et al., 2007) and possibly due to intensification of microsite differences with drought. Elevated growth plasticity may be advantageous in arid sites where precipitation is also highly unpredictable. In fact, growth bimodality in *Q. ilex* seems to be a plastic response to shifts in autumn precipitation (Gutiérrez et al., 2011). This bimodal behavior includes not only radial growth resumption after the release of summer drought, but also the formation of new shoots which correspond to the increased Sm variance at decreasing water availability in the evergreen oak. However, it is important to note that the consequences of increased variability in growth are not trivial, as they have been found to be positively related to drought legacies (Gazol et al., 2020).

Table 4

Results of mixed-effects models evaluating covariation between morphological traits and basal area increment (BAI) with variables integrated at tree- and site-levels. Standardized coefficients (confidence interval) and significance level (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) of are shown only for significant fixed effects. Coefficients of the main effect of SPEI are not shown, as they are identical to those in Table 2. In tree-level models, $T_{IC/IR}$ was variables were not included (*n.i.*).

Scale	Species	Trait	Mean	$T_{IC/IR}$	Mean x SPEI
Tree-level	Evergreen	LA		*n.i.*	
		Sm		*n.i.*	
		LMA	−0.07 (−0.05 to −0.02)*	*n.i.*	
		Sm:Lm		*n.i.*	
	Deciduous	LA		*n.i.*	
		Sm	0.06 (0.02 to 0.14)**	*n.i.*	−0.07 (−0.024 to −0.10)**
		LMA		*n.i.*	
		Sm:Lm	0.11 (0.01 to 0.22)***	*n.i.*	−0.16 (−0.19 to −0.14)***
Site-level	Evergreen	LA	0.10 (0.04 to 0.23)*	0.09 (0.02 to 0.19)*	
		Sm	0.15 (0.03 to 0.32)**		
		LMA		0.08 (0.04 to 0.19)*	
		Sm:Lm	0.06 (0.01 to 0.17)*		
	Deciduous	LA			
		Sm	0.17 (0.02 to 0.32)**		−0.09 (−0.14 to −0.05)*
		LMA			
		Sm:Lm	0.14 (0.04 to 0.24)***		−0.12 (−0.16 to −0.09)***

4.3. Drought performance is modulated by morphological traits

Recent studies have addressed the relationship between ITV and tree growth responses to drought (González de Andrés et al., 2021; Serra-Maluquer et al., 2021) or drought-induced tree mortality (Anderegg and HilleRisLambers, 2016; Kerr et al., 2022). Nevertheless, to our knowledge, this is the first evaluation of the covariation between functional traits and radial growth with a dual approach (spatial and temporal), thus overcoming the limitations due to the use of trait databases based on measurements at a single point in time. Hydraulic traits have been argued to better predict cross-species (Choat et al., 2012; Anderegg et al., 2016; Serra-Maluquer et al., 2022) and within-species drought performance patterns (González de Andrés et al., 2021; Kerr et al., 2022). However, the sensitivity and complexity of measuring these traits enlarge measurement effort and error, offsetting the advantages of including them in growth models (Li et al., 2022). In *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota*, we found that covariation of traits and growth emerges mainly at large spatial scales. Meanwhile, *Q. faginea/Q. humilis* showed similar relationships at tree- and site-levels (Table 4; Fig. 5a–c). Therefore, our third hypothesis only holds true for the evergreen species. Tighter coordination between traits and growth is observed under dry conditions, where conservative resource use traits (low LA and Sm and high LMA) are associated with low growth rates (Reich, 2014; Bena-vides et al., 2021; Vicente et al., 2022). Nevertheless, rather than a mechanistic link between growth and morphological traits within-species, our results may indicate common ecological drivers.

An outstanding and novel finding of this study is the relationship of trait variance with annual BAI and growth responses to drought. Although this issue has been widely discussed in the literature, it has rarely been empirically established in mature forests before. We observed a positive covariation between the spatial population variance (among trees within a site) of LA and LMA and radial growth of *Q. ilex* ssp. *ilex/Q. ilex* ssp. *ballota* was observed (Fig. 5d and e). From a mechanistic standpoint, high trait variation in leaf traits would increase the probability that at least some trees are able to effectively cope with unpredictable environmental conditions (Valladares et al., 2014; Anderegg et al., 2021), so improving population adjustment capacity. Plastic adjustments of leaf water potential regulation and drought tolerance have been proposed to maintain turgor and carbon assimilation in *Q. ilex* under moderate drought for longer periods of time (Limousin et al., 2022). Furthermore, higher trait variation among trees shapes populations with increased functional diversity that may prompt facilitation and/or niche partitioning (Forrester and Bauhus, 2016). Functional diversity has been related to enhanced productivity

(Pretzsch et al., 2015), more temporally stable growth (del Río et al., 2017), or higher resistance and resilience to drought (Gazol and Camarero, 2016). However, the covariation found between individuals within a site may also reflect common drought constraints on trait variance and radial growth. Therefore, future research is needed to further explore the relationships between trait variation within species and tree performance including a broader set of functional traits and higher number of tree species.

Finally, we found positive relationships between temporal trait variance of LA, Sm and Sm:Lm and resistance and resilience against an extreme drought-event in deciduous oaks (Fig. 6). This suggests that higher phenotypic plasticity in primary growth improves tree drought performance against extreme events such as droughts as previously suggested (Nicotra et al., 2010; Funk et al., 2017). Indeed, Challis et al. (2022) have recently described increased time to hydraulic failure related to high plasticity in hydraulic traits in response to shifts in soil water availability. Deciduous oak populations experiencing the most arid conditions are those showing lower ITV, which may result in a more conservative growth response to warmer and drier conditions. However, caution is needed when establishing cause-effect relationships since covariation may arise from common ecological drivers rather than mechanistic linkages. In this respect, reciprocal transplanting experiments may help to clarify these findings.

5. Conclusions

Our study demonstrates that the highest intraspecific variation in traits along a wide spatiotemporal gradient in Mediterranean oaks with contrasting foliar habit occurs within-individuals, indicating a high role of phenotypic plasticity in the total ITV. Through the analysis of a spatially and temporally explicit database, we were able to identify consistent trait adjustments toward more water-conservative trait values as conditions became drier. Significantly, trait variances also varied along water availability gradients showing stronger climatic filtering associated with increasing aridity, particularly in the more mesic deciduous oaks. These findings support the tradeoff between increased drought tolerance and the ability to handle variability in water availability by means of increased ITV. Drought constraints on trait variance primarily affected LMA in the evergreen *Q. ilex* spp. *ilex/Q. ilex* ssp. *ballota* and on LA, Sm and Sm:Lm in the deciduous *Q. faginea/Q. humilis*. Interestingly, these were the same traits that showed covariation with tree performance for foliar habit. Thus, evergreen oak populations with greater among-tree variability in LMA exhibited greater radial growth, while deciduous oak trees with greater plasticity in primary growth
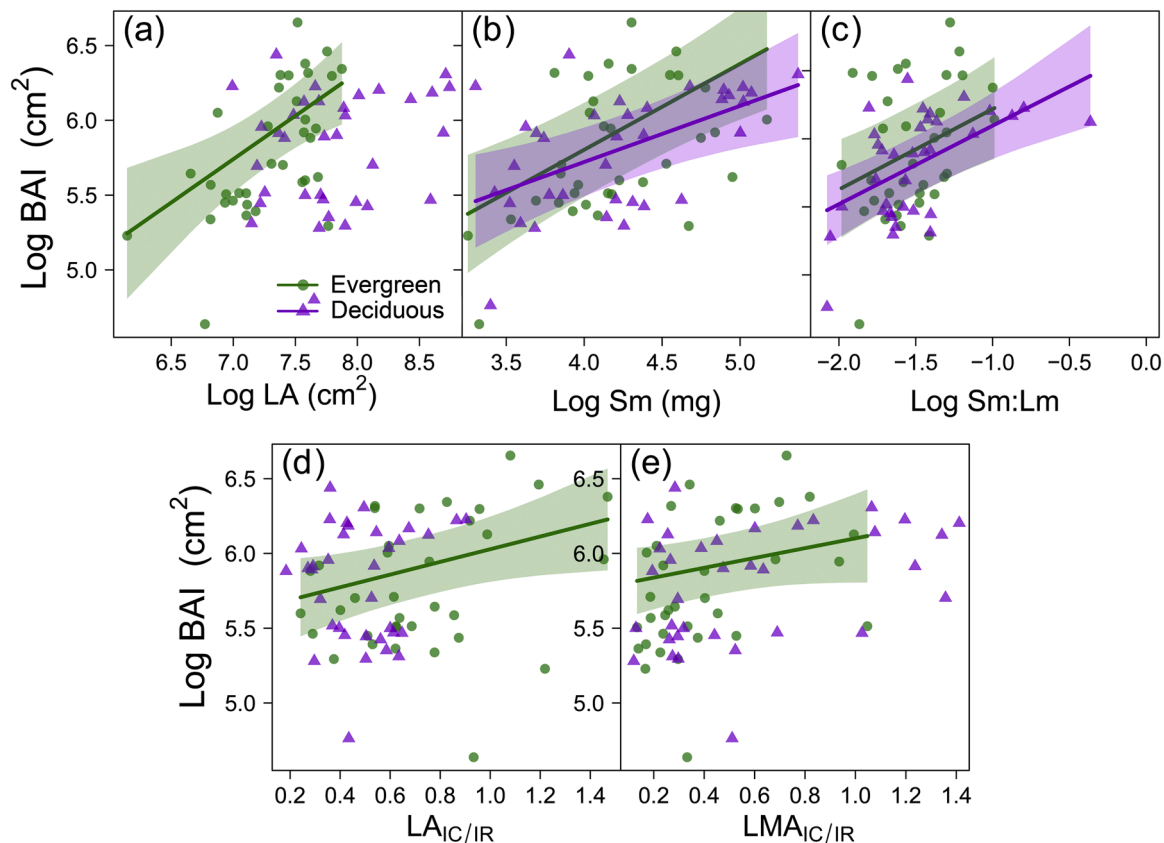
Fig. 5. Covariation between basal area increment (BAI) and morphological traits in evergreen oaks (green symbols and lines) and deciduous oaks (purple symbols and lines). Predictor variables are mean trait values (a-c) and trait variances (d-e). Solid lines represent significant effects according to linear mixed-effects models (see Table 4) and shaded areas are 95 % confidence intervals.
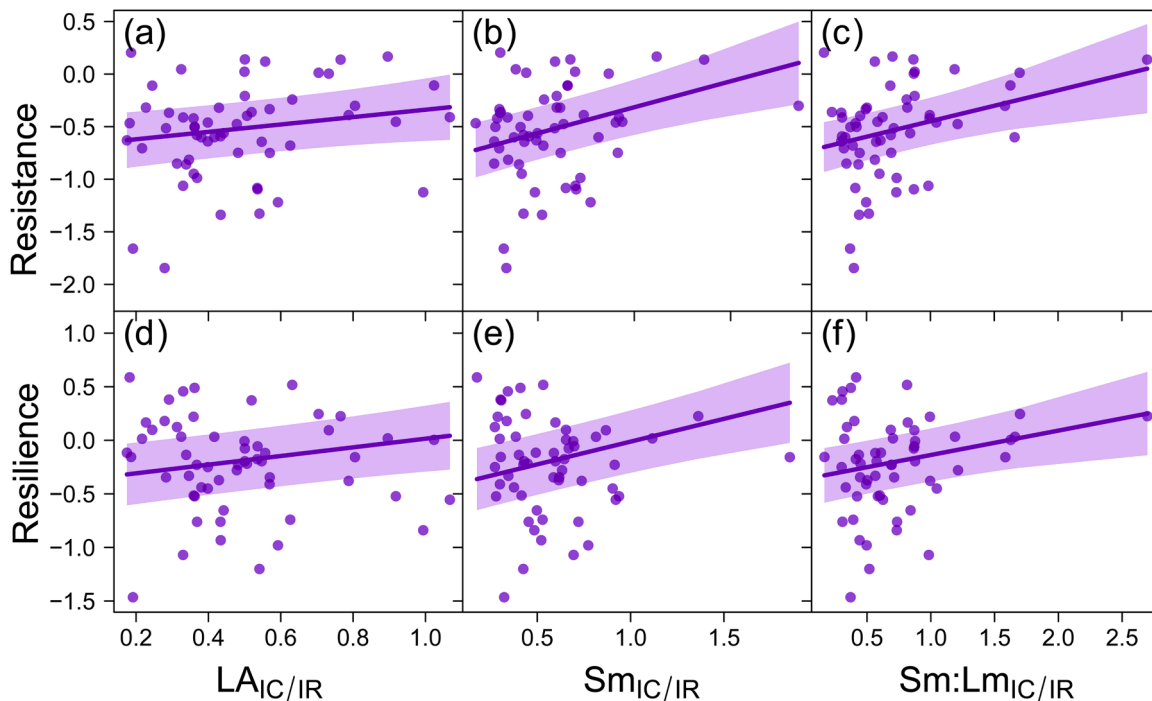

Fig. 6. Relationship between drought resistance (a-c) and resilience (d-f) indices and among-years trait variance (temporal $T_{IC/IR}$) of populations of deciduous oak species (*Quercus faginea* and *Q. humilis*). Solid lines represent significant effects according to linear mixed-effects models (see Table S5) and shaded areas are 95 % confidence intervals.

were more resistant and resilient to drought.

CRediT authorship contribution statement

Ester González de Andrés: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Xavier Serra-Maluquer:** Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Antonio Gazol:** Methodology, Formal analysis, Writing – review & editing. **José Miguel Olano:** Methodology, Writing – review & editing. **José Ignacio García-Plazaola:** Methodology, Writing – review & editing. **Beatriz Fernández-Marín:** Methodology, Writing – review & editing. **J. Bosco Imbert:** Methodology, Writing – review & editing. **Lluís Coll:** Methodology, Writing – review & editing. **Aitor Ameztegui:** Methodology, Writing – review & editing. **Josep Maria Espelta:** Methodology, Writing – review & editing. **Arben Q. Alla:** Methodology, Writing – review & editing. **J. Julio Camarero:** Conceptualization, Data curation, Methodology, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available from the Zenodo Repository: https://doi.org/10.5281/zenodo.7746627 (González de Andrés et al., 2023).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109884.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Alía, R., García del Barrio, J.M., Iglesias, S., Mancha, J.A., de Miguel, J., Nicolás, J.L., Pérez, F., Sánchez de Ron, D., 2009. Regiones De Procedencia De Especies Forestales De España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, Spain.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., Lavorel, S., 2010. Intraspecific functional variability: extent, structure and sources of variation. J. Ecol. 98, 604–613. https://doi.org/10.1111/j.1365-2745.2010.01651.x.

Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G., Violle, C., 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspect. Plant Ecol. Evol. Syst. 13, 217–225. https://doi.org/10.1016/j.ppees.2011.04.003.

Anderegg, L.D.L., HilleRisLambers, J., 2016. Drought stress limits the geographic ranges of two treespecies via different physiological mechanisms. Glob. Cheng. Biol. 22, 1029–1045. https://doi.org/10.1111/gcb.13148.

Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B., Jansen, S., 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc. Natl. Acad. Sci. U.S.A. 113, 5024–5029. https://doi.org/10.1073/pnas.1525678113.

Anderegg, L.D.L., Loy, X., Markham, I.P., Elmer, C.M., Hovenden, M.J., HilleRisLambers, J., Mayfield, M.M., 2021. Aridity drives coordinated trait shifts but not decreased trait variance across the geographic range of eight Australian trees. N. Phytol. 229, 1375–1387. https://doi.org/10.1111/nph.16795.

Anderegg, W.R.L., 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. New Phytol. 205, 1008–1014. https://doi.org/10.1111/nph.12907.

Andreu, L., Gutiérrez, E., Macias, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. Glob. Chang. Biol. 13, 804–815. https://doi.org/10.1111/j.1365-2486.2007.01322.x.

Babst, F., Bodesheim, P., Charney, N., Friend, A.D., Girardin, M.P., Klesse, S., Moore, D.J. P., Seftigen, K., Björklund, J., Bouriaud, O., Dawson, A., DeRose, R.J., Dietze, M.C., Eckes, A.H., Enquist, B., Frank, D.C., Mahecha, M.D., Poulter, B., Record, S., Trouet, V., et al., 2018. When tree rings go global: challenges and opportunities for retro- and prospective insight. Quat. Sci. Rev. 197, 1–20. https://doi.org/10.1016/j.quascirev.2018.07.009.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.48550/arXiv.1406.5823.

Benavides, R., Carvalho, B., Matesanz, S., Bastias, C.C., Cavers, S., Escudero, A., Fonti, P., Martínez-Sancho, E., Valladares, F., 2021. Phenotypes of Pinus sylvestris are more coordinated under local harsher conditions across Europe. J. Ecol. 109, 2580–2596. https://doi.org/10.1111/1365-2745.13668.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res. 64, 81–96. https://doi.org/10.3959/2008-6.1.

Bloomfield, K.J., Cernusak, L.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Wright, I.J., Boer, M.M., Bradford, M.G., Cale, P., Cleverly, J., Egerton, J.J.G., Evans, B.J., Hayes, L.S., Hutchinson, M.F., Liddell, M.J., Macfarlane, C., Meyer, W.S., Prober, S. M., Togashi, H.F., Wardlaw, T., et al., 2018. A continental-scale assessment of variability in leaf traits: within species, across sites and between seasons. Funct. Ecol. 32, 1492–1506. https://doi.org/10.1111/1365-2435.13097.

Borghetti, M., Gentilesca, T., Leonardi, S., Van Noije, T., Rita, A., 2017. Long-term temporal relationships between environmental conditions and xylem functional traits: a meta-analysis across a range of woody species along climatic and nitrogen deposition gradients. Tree Physiol. 37, 4–17. https://doi.org/10.1093/treephys/tpw087.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2020. dplR: Dendrochronology Program Library in R. R Package Version 1.7.1.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer-Verlag, New York.

Camarero, J.J., Olano, J.M., Arroyo Alfaro, S.J., Fernández-Marín, B., Becerril, J.M., García-Plazaola, J.I., 2012. Photoprotection mechanisms in Quercus ilex under contrasting climatic conditions. Flora 207, 557–564. https://doi.org/10.1016/j.flora.2012.06.003.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S.M., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. J. Ecol. 103, 44–57. https://doi.org/10.1111/1365-2745.12295.

Camarero, J.J., Sangüesa-Barreda, G., Vergarechea, M., 2016. Prior height, growth, and wood anatomy differently predispose to drought-induced dieback in two Mediterranean oak speciesk. Ann. For. Sci. 73, 341–351. https://doi.org/10.1007/s13595-015-0523-4.

Castro-Díez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M., Montserrat-Martí, G., 1997. Leaf morphology and leaf chemical composition in three Quercus (Fagaceae) species along a rainfall gradient in NE Spain. Trees - Struct. Funct. 11, 127–134. https://doi.org/10.1007/s004680050068.

Challis, A., Blackman, C., Ahrens, C., Medlyn, B., Rymer, P., Tissue, D., 2022. Adaptive plasticity in plant traits increases time to hydraulic failure under drought in a foundation tree. Tree Physiol. 42, 708–721. https://doi.org/10.1093/treephys/tpab096.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Field, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., et al., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688.

Coll, L., Camarero, J.J., Martínez de Aragón, J., 2012. Fine roots seasonal dynamics, plasticity and mycorrhization in two coexisting Mediterranean oaks with contrasting aboveground phenology. Ecoscience 19, 238–245. https://doi.org/10.2980/19-3-3488.

Cope, O.L., Burkle, L.A., Croy, J.R., Mooney, K.A., Yang, L.H., Wetzel, W.C., 2022. The role of timing in intraspecific trait ecology. Trend. Ecol. Evolut. 37, 997–1005. https://doi.org/10.1016/j.tree.2022.07.003.

Corcuera, L., Camarero, J.J., Gil-Pelegrín, E., 2004a. Effects of a severe drought on growth and wood anatomical properties of Quercus faginea. IAWA J. 25, 185–204. https://doi.org/10.1163/22941932-90000360.

Corcuera, L., Camarero, J.J., Gil-Pelegrín, E., 2004b. Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. *Trees - Struct. Funct.* 18, 83–92. https://doi.org/10.1007/s00468-003-0284-9.

Cornes, R., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An ensemble version of the E-OBS temperature and precipitation datasets. J. Geophys. Res.: Atmos. 123, 9391–9409. https://doi.org/10.1029/2017JD028200.

de Rigo, D., Caudullo, G., Durrant, T.H., San-Miguel-Ayanz, J., 2016. The European Atlas of Forest Tree Species: modelling, data and information on forest tree species. The European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg, pp. 40–45.

del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matovic, B., Mohren, F., et al., 2017. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris–Fagus sylvatica* mixtures across Europe. J. Ecol. 105, 1032–1043. https://doi.org/10.1111/1365-2745.12727.

Duursma, R.A., Falster, D.S., 2016. Leaf mass per area, not total leaf area, drives differences in above-ground biomass distribution among woody plant functional types. New Phytol. 212, 368–376. https://doi.org/10.1111/nph.14033.

Dwyer, J.M., Hobbs, R.J., Mayfield, M.M., 2014. Specific leaf area responses to environmental gradients through space and time. Ecology 95, 399–410. https://doi.org/10.1890/13- 0412.1.

Fajardo, A., Piper, F.I., 2011. Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. New Phytol. 189, 259–271. https://doi.org/10.1111/j.1469-8137.2010.03468.x.

Fajardo, A., Siefert, A., 2016. Phenological variation of leaf functional traits within species. Oecologia 180, 951–959. https://doi.org/10.1007/s00442-016-3545-1.

Forrester, D.I., Bauhus, J., 2016. A Review of processes behind diversity—Productivity relationships in forests. Curr. Forest. Rep. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Fréjaville, T., Benito Garzón, M., 2018. The EuMedClim database: yearly climate data (1901-2014) of 1 km resolution grids for Europe and the Mediterranean Basin. Front. Ecol. Evol. 6, 1–5. https://doi.org/10.3389/fevo.2018.00031.

Fritts, H.C., 2001. Tree Rings and Climate. Blackburn Press, Caldwell, USA.

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., Laughlin, D.C., Sutton-Grier, A.E., Williams, L., Wright, J., 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol. Rev. 92, 1156–1173. https://doi.org/10.1111/brv.12275.

García-Cervigón, A.I., Camarero, J.J., Cueva, E., Espinosa, C.I., Escudero, A., 2020. Climate seasonality and tree growth strategies in a tropical dry forest. J. Veg. Sci. 31, 266–280. https://doi.org/10.1111/jvs.12840.

Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. J. Ecol. 104, 1063–1075. https://doi.org/10.1111/1365-2745.12575.

Gazol, A., Camarero, J.J., Sánchez-Salguero, R., Vicente-Serrano, S.M., Serra-Maluquer, X., Gutiérrez, E., de Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martínez del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Hereş, A.M., et al., 2020. Drought legacies are short, prevail in dry conifer forests and depend on growth variability. J. Ecol. 108, 2473–2484. https://doi.org/10.1111/1365-2745.13435.

Gil-Pelegrín, E., Saz, M.A., Cuadrat, J.M., Peguero-Pina, J.J., & Sancho-Knapik, D. (2017). Oaks under Mediterranean-type climates: functional response to summer aridity. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D, eds. *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L. Cham: Tree Physiology*, vol 7. Springer, Cham.

González de Andrés, E., Rosas, T., Camarero, J.J., Martínez-Vilalta, J., 2021. The intraspecific variation of functional traits modulates drought resilience of European beech and pubescent oak. J. Ecol. 109, 3652–3669. https://doi.org/10.1111/1365-2745.13743.

Gutiérrez, E., Campelo, F., Camarero, J.J., Ribas, M., Muntán, E., Nabais, C., Freitas, H., 2011. Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. *Trees - Struct. Funct.* 25, 637–646. https://doi.org/10.1007/s00468-011-0540-3.

Herrera, C.M., 2017. The ecology of subindividual variability in plants: patterns, processes, and prospects. Web. Ecol. 17, 51–64. https://doi.org/10.5194/we-17-51-2017.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

IPCC, 2021. Summary for Policymakers, in: Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (Eds.), Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 3−32.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020. https://doi.org/10.1111/j.1461-0248.2005.00796.x.

Kannenberg, S.A., Novick, K.A., Alexander, M.R., Maxwell, J.T., Moore, D.J.P., Phillips, R.P., Anderegg, W.R.L., 2019. Linking drought legacy effects across scales: from leaves to tree rings to ecosystems. Glob. Chang. Biol. 25, 2978–2992. https://doi.org/10.1111/gcb.14710.

Kerr, K.L., Anderegg, L.D.L., Zenes, N., Anderegg, W.R.L., 2022. Quantifying within-species trait variation in space and time reveals limits to trait-mediated drought response. Funct. Ecol. 36, 2399–2411. https://doi.org/10.1111/1365-2435.14112.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Statist. Softw.2 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

López, R., Cano, F.J., Martin-StPaul, N.K., Cochard, H., Choat, B., 2021. Coordination of stem and leaf traits define different strategies to regulate water loss and tolerance ranges to aridity. N. Phytol. 230, 497–509. https://doi.org/10.1111/nph.17185.

Li, Y., Jiang, Y., Zhao, K., Chen, Y., Wei, W., Shipley, B., Chu, C., 2022. Exploring trait–performance relationships of tree seedlings along experimentally manipulated light and water gradients. Ecology 103, 1–13. https://doi.org/10.1002/ecy.3703.

Limousin, J.M., Roussel, A., Rodríguez-Calcerrada, J., Torres-Ruiz, J.M., Moreno, M., García de Jalón, L., Ourcival, J.M., Simioni, G., Cochard, H., Martin-StPaul, N., 2022. Drought acclimation of *Quercus ilex* leaves improves tolerance to moderate drought but not resistance to severe water stress. Plant Cell Environ. 45, 1967–1984. https://doi.org/10.1111/pce.14326.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J.F. J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U., Zweifel, R., 2009. Hydraulic adjustment of Scots pine across Europe. N. Phytol. 184, 353–364. https://doi.org/10.1111/j.1469-8137.2009.02954.x.

Mendiavilla, S., Martín, I., Babiano, J., Escudero, A., 2019. Foliar plasticity related to gradients of heat and drought stress across crown orientations in three Mediterranean *Quercus* species. PLoS One 14, e0224462. https://doi.org/10.1371/journal.pone.0224462.

Messier, J., McGill, B.J., Lechowicz, M.J., 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecol. Lett. 13, 838–848. https://doi.org/10.1111/j.1461-0248.2010.01476.x.

Messier, J., McGill, B.J., Enquist, B.J., Lechowicz, M.J., 2017. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? Ecography 40, 685–697. https://doi.org/10.1111/ecog.02006.

Montserrat-Martí, G., Camarero, J.J., Palacio, S., Pérez-Rontomé, C., Milla, R., Albuixech, J., Maestro, M., 2009. Summer-drought constrains the phenology and growth of two coexisting Mediterranean oaks with contrasting leaf habit: implications for their persistence and reproduction. *Trees - Struct. Funct.* 23, 787–799. https://doi.org/10.1007/s00468-009-0320-5.

Moore, T.E., Jones, C.S., Chong, C., Schlichting, C.D., 2020. Impact of rainfall seasonality on intraspecific trait variation in a shrub from a Mediterranean climate. Funct. Ecol. 34, 865–876. https://doi.org/10.1111/1365-2435.13533.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trend. Plant Sci. 15, 684–692. https://doi.org/10.1016/j.tplants.2010.09.008.

Niinemets, Ü., 2015. Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll *Quercus ilex*. New Phytol. 205, 79–96. https://doi.org/10.1111/nph.13001.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., et al., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225.

Peguero-Pina, J.J., Sancho-Knapik, D., Barrón, E., Camarero, J.J., Vilagrosa, A., Gil-Pelegrín, E., 2014. Morphological and physiological divergences within *Quercus ilex* support the existence of different ecotypes depending on climatic dryness. Ann. Bot. 114, 301–313. https://doi.org/10.1093/aob/mcu108.

Peguero-Pina, J.J., Sisó, S., Sancho-Knapik, D., Díaz-Espejo, A., Flexas, J., Galmés, J., Gil-Pelegrín, E., 2016. Leaf morphological and physiological adaptations of a deciduous oak (*Quercus faginea* Lam.) to the Mediterranean climate: a comparison with a closely related temperate species (*Quercus robur* L.). Tree Physiol. 36, 287–299. https://doi.org/10.1093/treephys/tpv107.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and S-PLUS. Springer-Verlag, New York.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2020. _nlme: Linear and Nonlinear Mixed Effects Models_. R package Version 3.1-145.

Poorter, H., Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. N. Phytol. 182, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x.

Power, S.C., Verboom, G.A., Bond, W.J., Cramer, M.D., 2019. Does a tradeoff between trait plasticity and resource conservatism contribute to the maintenance of alternative stable states? N. Phytol. 223, 1809–1819. https://doi.org/10.1111/nph.15981.

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matovic, B., Mohren, F., et al., 2015. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. Eur. J. For. Res. 134, 927–947. https://doi.org/10.1007/s10342-015-0900-4.

R core Team, 2022. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ramírez-Valiente, J.A., Cavender-Bares, J., 2017. Evolutionary trade-offs between drought resistance mechanisms across a precipitation gradient in a seasonally dry tropical oak (*Quercus oleoides*). Tree Physiol. 37, 889–901. https://doi.org/10.1093/treephys/tpx040.

Ramírez-Valiente, J.A., Valladares, F., Delgado, A., Nicotra, A.B., Aranda, I., 2015. Understanding the importance of intrapopulation functional variability and phenotypic plasticity in *Quercus suber*. Tree Genet. Genom. 11, 1–11. https://doi.org/10.1007/s11295-015-0856-z.

Ramírez-Valiente, J.A., López, R., Hipp, A.L., Aranda, I., 2020. Correlated evolution of morphology, gas exchange, growth rates and hydraulics as a response to precipitation and temperature regimes in oaks (*Quercus*). N. Phytol. 227, 794–809. https://doi.org/10.1111/nph.16320.

Reich, P.B., Luo, Y., Bradford, J.B., Poorter, H., Perry, C.H., Oleksyn, J., 2014. Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. Proc. Natl. Acad. Sci. U.S.A. 111, 13721–13726. https://doi.org/10.1073/pnas.1216053111.

Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301. https://doi.org/10.1111/1365-2745.12211.

Resco de Dios, V., Arteaga, C., Peguero-Pina, J.J., Sancho-Knapik, D., Qin, H., Zveushe, O.K., Sun, W., Williams, D.G., Boer, M.M., Voltas, J., Moreno, J.M., Tissue, D.T., Gil-Pelegrín, E., 2020. Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks. Plant Cell Environ. 43, 1944–1957. https://doi.org/10.1111/pce.13781.

Rosas, T., Mencuccini, M., Barba, J., Cochard, H., Saura-Mas, S., Martínez-Vilalta, J., 2019. Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. N. Phytol. 223, 632–646. https://doi.org/10.1111/nph.15684.

Rubio de Casas, R., Vargas, P., Pérez-Corona, E., Manrique, E., Quintana, J.R., García-Verdugo, C., Balaguer, L., 2007. Field patterns of leaf plasticity in adults of the long-lived evergreen *Quercus coccifera*. Ann. Bot. 100, 325–334. https://doi.org/10.1093/aob/mcm112.

Salazar Zarzosa, P., Diaz Herraiz, A., Olmo, M., Ruiz-Benito, P., Barrón, V., Bastias, C.C., de la Riva, E.G., Villar, R., 2021. Linking functional traits with tree growth and forest productivity in *Quercus ilex* forests along a climatic gradient. Sci. Total Environ. 786, 147468 https://doi.org/10.1016/j.scitotenv.2021.147468.

Schmitt, S., Trueba, S., Coste, S., Ducouret, É., Tysklind, N., Heuertz, M., Bonal, D., Burban, B., Hérault, B., Derroire, G., 2022. Seasonal variability of leaf thickness: an overlooked component of functional trait variability. Plant Biol. 24, 458–463. https://doi.org/10.1111/plb.13395.

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

Seidl, R., Thom, D., Kautz, M., Martín-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mariota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7, 395–402. https://doi.org/10.1038/nclimate3303.

Serra-Maluquer, X., Granda, E., Camarero, J.J., Vilà-Cabrera, A., Jump, A.S., Sánchez-Salguero, R., Sangüesa-Barreda, G., Imbert, J.B., Gazol, A., 2021. Impacts of recurrent dry and wet years alter long-term tree growth trajectories. J. Ecol. 109, 1561–1574. https://doi.org/10.1111/1365-2745.13579.

Serra-Maluquer, X., Gazol, A., Anderegg, W.R.L., Martínez-Vilalta, J., Mencuccini, M., Camarero, J.J., 2022. Wood density and hydraulic traits influence species' growth response to drought across biomes. Glob. Chang. Biol. 28, 3871–3882. https://doi.org/10.1111/gcb.16123.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M.V., Dantas, V.L., de Bello, F., Duarte, L.D.S., Fonseca, C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., et al., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol. Lett. 18, 1406–1419. https://doi.org/10.1111/ele.12508.

Solé-Medina, A., Robledo-Arnuncio, J.J., Ramírez-Valiente, J.A., 2022. Multi-trait genetic variation in resource-use strategies and phenotypic plasticity correlates with local climate across the range of a Mediterranean oak (*Quercus faginea*). N. Phytol. 234, 462–478. https://doi.org/10.1111/nph.17968.

Stotz, G.C., Salgado-Luarte, C., Escobedo, V.M., Valladares, F., Gianoli, E., 2021. Global trends in phenotypic plasticity of plants. Ecol. Lett. 24, 2267–2281. https://doi.org/10.1111/ele.13827.

Taudiere, A., Violle, C., 2016. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. Ecography 39, 699–708. https://doi.org/10.1111/ecog.01433.

Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. Geogr. Rev. 38, 55–94. https://doi.org/10.2307/2107309.

Tumajer, J., Serra-Maluquer, X., Gazol, A., González de Andrés, E., Colangelo, M., Sangüesa-Barreda, G., Olano, J.M., Rozas, V., García-Plazaola, J.I., Fernández-Marín, B., Imbert, J.B., Coll, L., Ameztegui, A., Espelta, J.M., Alla, A.Q., Campelo, F., Camarero, J.J., 2022. Bimodal and unimodal radial growth of Mediterranean oaks along a coast-inland gradient. Agric. For. Meteorol. 327, 109234 https://doi.org/10.1016/j.agrformet.2022.109234.

Valladares, F., Gianoli, E., Gómez, J.M., 2007. Ecological limits to plant phenotypic plasticity. N. Phytol. 176, 749–763. https://doi.org/10.1111/j.1469-8137.2007.02275.x.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. 17, 1351–1364. https://doi.org/10.1111/ele.12348.

van Bodegom, P.M., Douma, J.C., Verheijen, L.M., 2014. A fully traits-based approach to modeling global vegetation distribution. Proc. Natl. Acad. Sci. U.S.A. 111, 13733–13738. https://doi.org/10.1073/pnas.1304551110.

Vasey, G.L., Weisberg, P.J., Urza, A.K., 2022. Intraspecific trait variation in a dryland tree species corresponds to regional climate gradients. J. Biogeogr. 49, 2309–2320. https://doi.org/10.1111/jbi.14515.

Vicente, E., Didion-Gency, M., Morcillo, L., Morin, X., Vilagrosa, A., Grossiord, C., 2022. Aridity and cold temperatures drive divergent adjustments of European beech xylem anatomy, hydraulics and leaf physiological traits. Tree Physiol. 42, 1720–1735. https://doi.org/10.1093/treephys/tpac029.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.

Vicente-Serrano, S.M., Tomas-Burguera, M., Beguería, S., Reig, F., Latorre, B., Peña-Gallardo, M., Luna, M.Y., Morata, A., González-Hidalgo, J.C., 2017. A high resolution dataset of drought indices for Spain. Data 2, 1–10. https://doi.org/10.3390/data2030022.

Villar-Salvador, P., Castro-Díez, P., Pérez-Rontomé, C., Montserrat-Martí, G., 1997. Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees - Struct. Funct.* 12, 90–96. https://doi.org/10.1007/s004680050126.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. Trend. Ecol. Evolut. 27, 244–252. https://doi.org/10.1016/j.tree.2011.11.014.

Westerband, A.C., Funk, J.L., Barton, K.E., 2021. Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. Ann. Bot. 127, 397–410. https://doi.org/10.1093/aob/mcab011.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornellssen, J.H.C., Diemer, M., Lexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., et al., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.

Zhou, S., Zhang, Y., Williams, A.P., Gentine, P., 2019. Projected increases in intensity, frequency, and terrestrial carbon costs of compound drought and aridity events. Sci. Adv. 5, 1–9. https://doi.org/10.1126/sciadv.aau5740.