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REVIEW

Functional mechanisms and drought responses in Mediterranean oaks: three decades of research and a categorical synthesis

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Abstract

Key message **Drought resistance and resilience in Mediterranean oaks appear to be structured along axes of variation linked to leaf habit and wood anatomy.**

Abstract Recurrent and intensifying droughts have emerged as a principal driver of decline in Mediterranean oak forests over the past three decades. This review synthesizes current understanding of the functional mechanisms shaping drought impacts in these ecosystems and complements existing work by combining a structured categorical overview with a multivariate functional ordination of oak responses. We assembled a dataset of 240 records derived from 212 studies published between 1994 and 2024, spanning species with contrasting leaf habits (evergreen, deciduous, semi-persistent), diverse wood anatomies (diffuse-, ring-, and semi-ring-porous), and developmental stages ranging from seedlings to mature stands. The studies encompass a broad gradient of drought durations and intensities, enabling comparison of drought resistance and resilience across plant systems. Across the reviewed literature, key ecophysiological mechanisms include stomatal regulation, hydraulic and osmotic adjustment, morpho-anatomical plasticity, and phenological shifts. However, most studies investigate these mechanisms in isolation, and integrative, multi-trait analyses remain rare. Using coarse categorical metrics, we found no clear geographic structuring of resistance, resilience, or response mechanisms, likely reflecting uneven species representation and heterogeneous experimental designs. Nonetheless, the dataset reveals functional patterns linked to plant diversity: deciduous, ring-porous species exhibit higher frequencies of low-resistance and low-resilience states, whereas evergreen, diffuse-porous species tend to display greater hydraulic safety and recovery capacity. Correspondence analysis further highlights major axes of variation associated with leaf habit and wood anatomy, confirming divergent adaptive strategies among Mediterranean oak functional types. Collectively, these findings underscore the importance of functional diversity in shaping drought responses and provide a framework for future mechanistic research and climate-adapted forest management.

Keywords Tree · Forest · *Quercus* · Climate Change · Resilience

Introduction

The Mediterranean Basin is recognized as a global biodiversity hotspot, characterized by remarkable diversity of flora and fauna shaped by long-term biogeographic and historical processes. However, the region is vulnerable to climate change, exhibiting accelerated warming and an increased incidence of drought, even though long-term precipitation trends are spatially heterogeneous and not uniformly declining (Vicente-Serrano et al. 2025). The combined effects of rising temperatures and recurrent drought threaten ecosystem functioning, intensify pressures on biodiversity, and jeopardize key ecological processes (Myers et al. 2000; Lazoglou et al. 2024).

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Within this context, Mediterranean forests form a heterogeneous ecological mosaic, characterized by pronounced variation in species composition and community structure across altitudinal and edaphic gradients. At lower elevations, sclerophyllous evergreen species dominate forests and shrublands, displaying adaptations to drought and nutrient-poor soils, whereas supra-Mediterranean zones support deciduous and semi-persistent taxa better suited to cooler, more humid environments (Mariotti et al. 2018; Kavgacı et al. 2021).

Oaks (*Quercus* spp.), including evergreen, deciduous, and semi-persistent species – the latter retaining foliage through most of the year but shedding it seasonally – are key components of Mediterranean forests, where their interspecific and functional diversity underpins ecosystem productivity and resilience. This diverse oak assemblage has been shaped by post-glacial migration, anthropogenic disturbance, and ongoing evolutionary processes, with hybridization and introgression promoting local adaptation and enhancing the adaptive potential of populations, thereby generating extensive phenotypic variability and ecological plasticity (Kremer and Hipp 2020; Pütz et al. 2025).

Despite their ecological significance, oaks have exhibited sensitivity to episodic decline throughout the Mediterranean since the 1980s, manifested by reduced growth, diminished vitality, and increased mortality. The drivers of this decline are multifactorial and include pathogen outbreaks, insect infestations, land-use change, and, more recently, increasing climatic stress, particularly recurrent and extreme drought events (Gentilesca et al. 2017; Alderotti et al. 2024; Bose et al. 2024). Recent meta-analyses confirm that pathogens and climatic stressors, particularly drought, act as primary and interacting forces that amplify both the likelihood and the severity of decline (Carluccio et al. 2025; Marques et al. 2025).

Over the past three decades, research on Mediterranean oak has increasingly focused on drought-stress responses, employing approaches such as functional wood anatomy, dendrochronology, ecophysiology, and remote sensing. A broad consensus has emerged that drought events substantially reduce oak vitality, productivity, and resilience at both the individual and population levels; xylem hydraulic failure is recognized as the primary mechanism underlying drought-induced decline and mortality, consistent with widely reported findings (Choat et al. 2012; Colangelo et al. 2017; Gentilesca et al. 2017; Alday et al. 2020).

Climatic forcing also interacts with local edaphic and structural conditions to shape decline trajectories, and variation in drought responses has been observed among species differing in geographic range, phenology, and functional traits.This diversity reflects a spectrum of adaptive strategies integrating physiological and morphological mechanisms, including stomatal and hydraulic regulation, dynamic carbon allocation, fluctuations in non-structural carbohydrate reserves, root expansion with hydraulic redistribution, and phenological shifts such as leaf-area reduction and increased sclerophylly (Limousin et al. 2012; Adams et al. 2017; Moreno et al. 2024). These adaptations contribute to ecophysiological variability, which can hinder prediction of drought-induced mortality when based solely on hydraulic risk, unless analyses are integrated with functional traits, community composition, and environmental niche parameters (Sanchez-Martinez et al. 2023).

These findings motivated the present synthesis, which evaluates and integrates existing evidence on drought-response mechanisms in Mediterranean oaks and complements this narrative overview with a categorical dataset representing three decades of research and prevailing methodological approaches. The analysis identifies which components of drought response, levels of biological organization, and functional mechanisms have received the most attention, elucidates patterns of resistance and resilience associated with leaf habit and wood anatomy, and highlights key gaps in our understanding of ecological adaptation in these systems. Among the many traits influencing drought responses, leaf habit (evergreen, deciduous, semi-persistent) and wood anatomy (diffuse-, ring-, and semi-ring-porous xylem) emerge as two major axes of functional variation. Leaf habit is tightly linked to phenological patterns, carbon balance, and water-use strategies, whereas wood anatomical type constrains hydraulic efficiency and safety. Previous work has shown that these traits modulate drought-induced growth reductions and mortality risk in Mediterranean forests, making them particularly suitable for structuring our categorical synthesis (e.g. Galle et al. 2011; Borghetti et al. 2020; Castagneri et al. 2020).

Drought response mechanisms: a narrative synthesis

We conducted a systematic literature search using the Web of Science (Clarivate Analytics) database to identify publications from 1994 to 2024, applying the query "Quercus AND drought AND Mediterranean." The search returned more than 600 records, which were screened through title, abstract, and full-text evaluation.

Out of these, studies were retained for further analysis when they fulfilled the following criteria: (i) a primary focus on Mediterranean *Quercus* species; (ii) explicit investigation of drought, either through experimental manipulation (e.g. controlled water limitation) or along natural drought gradients; and (iii) provision of sufficiently detailed empirical data, clearly reported in tables, figures or quantitative descriptions, to allow assessment of relevant variables.

Studies were excluded when they did not meet these requirements, including: (i) research only marginally related to the Mediterranean region; (ii) purely modelling or conceptual papers without original empirical data; (iii) vegetation-survey, floristic or genetic studies lacking a clear ecophysiological focus; (iv) studies primarily addressing non-*Quercus* species; and (v) papers in which drought was not a central driver or explicitly analysed factor. After applying these criteria, 212 studies were retained for detailed analysis and dataset construction.

Seminal contributions published before 1994 were included when deemed substantially relevant to the topic. Articles published after 2024 were considered in the narrative synthesis but were not included in the analyzed categorical dataset.

The synthesis presented in this section offers a concise overview of the functional mechanisms underlying drought adaptation in Mediterranean oak species, as identified in the retrieved literature. The references cited here are not intended to provide exhaustive coverage but serve as illustrative examples supporting the concepts and findings discussed.

In the following narrative synthesis, we use the term resistance to denote the ability of a plant system (seedlings, individual trees, or stands) to maintain core physiological and ecological functions during drought, and resilience to denote its capacity to recover those functions after drought. We refer to systems as vulnerable when they exhibit low resistance and/or low resilience, typically expressed as repeated growth depressions, crown dieback, or increased mortality risk under recurrent drought. We further use drought legacies to describe persistent alterations in growth, structure, or physiological status that extend into subsequent years and modulate responses to later climatic events.

In parallel, a categorical dataset was compiled from the same pool of studies by selecting experiments that explicitly quantified drought effects on assimilation, vigour, or vitality, and provided sufficient information to assess drought duration, intensity, plant resistance, and resilience. Consequently, the categorical analysis constitutes a structured, semi-quantitative extension of the narrative synthesis, summarizing the prevalence of these mechanisms across studies and comparing them among functional groups.

Hydraulic regulation and metabolic responses

Mediterranean oak species, including *Q. ilex*, exhibit marked drought tolerance, primarily through anisohydric regulation, which sustains photosynthetic activity as leaf water potential declines. This strategy enables continued carbon assimilation under pronounced fluctuations in soil moisture and atmospheric evaporative demand, distinguishing oaks from co-occurring species with more isohydric behavior, such as *Q. suber*. Increasing evidence, however, indicates that iso/anisohydric behavior emerges from plant–environment interactions rather than representing a fixed species trait; species may shift along this continuum depending on water availability, stand composition, and competitive context (Garcia-Forner et al. 2017; Hochberg et al. 2018).

The capacity to maintain metabolic activity under water stress is closely linked to osmotic adjustment, involving increased accumulation of soluble carbohydrates and proline, which lowers cellular osmotic potential, sustains turgor, and supports physiological function during acute drought.

Beyond leaf-level effects, long-term drought experiments and metabolomic investigations on Mediterranean woody species, including *Quercus ilex*, reveal coordinated shifts in non-structural carbohydrate (NSC) pools and compatible solutes at the whole-tree level, indicating that NSC dynamics help buffer hydraulic risk and facilitate recovery (Rosas et al. 2013). However, as shown in *Q. ilex* and *Q. suber*, severe drought may cause persistent reductions in growth and incomplete post-drought recovery, associated with altered carbohydrate allocation, metabolite profiles, and sustained reductions in stomatal and mesophyll conductance, indicating that biochemical acclimation alone may not fully compensate for recurrent or extreme water deficits (Rosas et al. 2013; Almeida et al. 2020). These findings are in line with the high frequency of intermediate-to-strong impacts on assimilation and vitality summarized in our categorical dataset.

Morpho-anatomical plasticity

Anatomical and morphological adaptations, such as increased epicuticular wax deposition and spatially heterogeneous stomatal responses (stomatal patchiness), further optimize gas exchange and water-use efficiency during intermittent drought periods. These integrated physiological and morphological responses underpin the drought-tolerance strategies of Mediterranean oaks, yet current evidence also highlights limits to their resilience under recurrent or severe stress (Galle et al. 2011; Klein et al. 2013; Holland et al. 2016; Limousin et al. 2022).

Leaf shedding during intense drought represents a rapid adaptive mechanism that mitigates hydraulic dysfunction through selective loss of older or less efficient foliage, thereby reducing canopy transpiration and maintaining hydraulic integrity (Lloret et al. 2004; Castellaneta et al. 2022). While this response enhances short-term survival, recurrent drought can make defoliation and partial crown retrenchment chronic. Combined dendrochronological and remote-sensing analyses link repeated canopy greenness loss to reduced radial growth and elevated dieback

probability, indicating that traits such as drought-induced leaf shedding, partial crown retrenchment, and shifts in leaf area, which confer short-term hydraulic protection by reducing transpirational demand, may drive long-term structural decline when climate extremes interact with predisposing stand or site conditions (shallow or rocky soils, high stand density, or previous disturbance history (e.g. Serrano and Peñuelas 2005).

Over prolonged or recurrent drought, Mediterranean oaks undergo structural and functional acclimation, including the development of xeromorphic leaf traits such as higher leaf mass per area, thicker cuticles, and reduced lamina size. These sclerophyllous features limit water loss, enhance photoprotection and thermal buffering, and increase resistance to both abiotic and biotic stressors. Similar plastic responses – such as shifts in epicuticular waxes and increased stomatal encryption – in evergreen and semi-persistent species indicate that convergent morpho-anatomical strategies may underpin drought tolerance across contrasting leaf habits (Abrantes et al. 2013; Laoué et al. 2024).

Across the reviewed studies, xeromorphic adjustments were reported mainly for evergreen sclerophylls (notably *Quercus ilex* and related taxa). Although these traits are not expressed consistently across all drought-stressed individuals or species, and their occurrence could only be assessed qualitatively rather than quantitatively within our dataset, reduced resistance and resilience under intense or prolonged drought are also evident in oak species typically prone to structural and xylem-related adjustments.

Chronic water limitation also induces anatomical modifications that enhance hydraulic safety. These include narrower xylem vessels, higher vessel density, and altered pit membrane structure (increased thickness, reduced porosity), all of which reduce cavitation risk and limit embolism spread. Mediterranean oaks may further exhibit intra-annual xylem plasticity, reflected in density fluctuations that track environmental conditions. While these traits enhance hydraulic safety, they reduce hydraulic conductivity, revealing a fundamental trade-off between safety and transport efficiency that constrains drought tolerance (David et al. 2013; Balzano et al. 2020; Borghetti et al. 2020).

Architectural and phenological adjustments

Root architecture plays a central role in mediating drought tolerance. Root systems exhibit plasticity under recurring drought, reallocating biomass to deeper and more extensive structures that improve water uptake and promote post-drought recovery. Empirical and modeling studies consistently show that deep-rooted individuals can exploit subsoil water reserves that remain available when surface layers dry, thereby sustaining physiological activity during prolonged water deficits. Variation in access to deep soil water pools is a major determinant of heterogeneous drought-induced decline among coexisting individuals, with deeper or more hydraulically efficient rooting systems associated with lower dieback and higher growth resilience. In *Quercus suber*, this may take the form of a dimorphic root system composed of superficial roots and a central taproot branching into fine roots that access groundwater (Ripullone et al. 2020; Castellaneta et al. 2022).

At the canopy scale, Mediterranean oaks display plasticity in crown architecture, including adjustments in leaf area and branching patterns in response to drought. Leaf production shows temporal lags relative to water availability, decreasing after dry years and increasing following wet years. These responses balance light interception with water conservation, limiting evaporative losses while sustaining photosynthetic activity. Reduced canopy density also enhances air circulation and heat dissipation during heat waves, while flexible shoot growth and branching support carbon acquisition and hydraulic efficiency. Combined use of spectral indices, chlorophyll fluorescence, and high-resolution remote sensing enables effective tracking of spatiotemporal changes in stress and photosynthetic status, and the correspondence between remotely sensed canopy closure and radial growth offers a basis for forecasting productivity under prolonged drought (Lloret et al. 2004; Limousin et al. 2012; Gentilesca et al. 2017).

Growth phenology in Mediterranean oaks is tightly regulated by seasonal water availability. Active growth typically coincides with periods of higher soil moisture in spring and autumn, while summer drought restricts or halts growth. These patterns may appear as unimodal or bimodal annual cycles depending on climatic variability and site conditions. This temporal flexibility allows oaks to concentrate growth during intervals of reduced hydraulic risk, improving drought avoidance and resilience. Numerous dendroecological and stem-growth studies on Mediterranean oaks show that intra-annual and diurnal stem diameter variations tend to closely track fluctuations in soil moisture and water availability, providing a sensitive indicator of phenological responsiveness to Mediterranean climate regimes, however most evidence remains based on case studies, with limited systematic quantification across species and sites. Overall, phenological plasticity interacts with inherent rhythmic growth processes, enabling both evergreen and deciduous oaks to optimize growth windows and maintain productivity under climatic constraints (Camarero et al. 2015; Montserrat-Mart et al. 2009; Alday et al. 2020; Vieira et al. 2022; Campelo et al. 2023).

Severe drought events consistently produce substantial reductions in radial growth, delays in phenological activity, and incomplete canopy recovery. These impacts may

produce drought legacies, understood here as persistent alterations in growth, structure, or physiological condition that extend into subsequent years and shape responses to later climatic events. The effects of such legacies may persist for multiple growing seasons, with their duration and severity modulated by site conditions, functional traits, and antecedent climate. These persistent changes increase mortality risk and may predispose forest stands to progressive decline under recurrent or prolonged drought (Bose et al. 2024; Italiano et al. 2024).

Intraspecific variability and multi-trait drought strategies

Intraspecific variability plays a critical role in shaping drought resilience. This can arise at multiple hierarchical levels – among populations, tree cohorts and individuals – driven by genetic differences, epigenetic effects, and phenotypic plasticity which allows individuals to adjust growth and physiological processes to local conditions. Studies integrating genetic, functional trait, and ecological data reveal a diverse array of drought-response strategies, including differences in growth dynamics, leaf physiology, and water-use efficiency. This highlights the need for integrative frameworks that consider genetic diversity, trait variation, and environmental context when forecasting drought resilience. Evidence that marginal or rear-edge populations often exhibit distinct growth–climate relationships and vulnerability profiles compared with core populations reinforces the importance of multi-site, multi-level approaches to characterizing the adaptive landscape of drought responses in Mediterranean oaks (Mariotti et al. 2018; Stephan et al. 2018; Kremer and Hipp 2020; Alderotti et al. 2024).

Overall, Mediterranean oaks employ a suite of interconnected adaptive mechanisms – including stomatal regulation, biochemical adjustments, anatomical modifications, and phenological shifts – that together promote survival and facilitate recovery following drought. The coordinated deployment of these traits contributes to the ecological success and persistence of oak species and populations. However, mounting evidence indicates that this adaptive capacity is increasingly challenged by rising drought frequency and severity under climate change. Recurrent and more extreme droughts may overwhelm even well-coordinated, multi-trait strategies, ultimately reducing growth, compromising vitality, and delaying recovery (Gentilesca et al. 2017; Peguero-Pina et al. 2017; Italiano et al. 2024). This underscores the need for integrative frameworks that consider genetic diversity, trait variation, and environmental context when forecasting drought resilience (González de Andrés et al. 2021, 2024) and is synthesized conceptually in Fig. 1.

Categorical dataset: construction, description and analysis

Each of the 212 selected articles was thoroughly evaluated, and discrete scores were assigned to a predefined set of response categories. A categorical scoring scheme was adopted rather than a quantitative approach because the studies differed markedly in the species examined, plant material, experimental design, drought metrics, and reporting formats, making quantitative comparisons unreliable or infeasible. Accordingly, this approach is not intended to provide formal effect-size estimates; rather, it aims to distill broad, comparable patterns of drought responses across diverse experimental contexts.

Based on the overview presented in the previous section, several categories encompassing physiological processes, drought characteristics, and plant system responses were defined, each accompanied by explicit scoring criteria (Table 1). To ensure methodological rigour and minimize potential bias, all scoring was conducted by a single designated team member following a common calibration exercise. Nonetheless, the categorical nature of the dataset means that subtle quantitative differences among studies may not be captured, and the findings should be interpreted as semi-quantitative patterns rather than precise estimates.

A categorical dataset (provided as supplementary material, S1_dataset) was ultimately assembled. It includes 240 experimental records derived from 212 articles and encodes, for each record, the oak species investigated, leaf habit (evergreen, deciduous, semi-persistent), wood anatomy (diffuse-, ring-, or semi-ring-porous), and the geographic position and elevation of the study sites (latitude, longitude, altitude). Each record further specifies the plant system (seedlings, individual trees, or forest stands), as well as the duration (ranging from short-term, low-intensity to multi-year, severe treatments) and intensity of drought. Drought intensity was assessed based on the information available in the selected literature, including standardized drought indices, relative reductions in precipitation, and the magnitude of soil moisture deficits. The records also include the ecophysiological mechanisms evaluated (e.g., stomatal control, osmotic adjustment, leaf and xylem modifications, and coordinated multi-trait responses), together with categorical scores for drought effects on photosynthesis, vigour and vitality, and system resistance and resilience.

The dataset is dominated by *Q. ilex* (including *Q. ilex* subsp. *rotundifolia*), *Q. pubescens*, *Q. suber*, *Q. faginea*, *Q. pyrenaica* (including *Q. subpyrenaica*), *Q. cerris*, *Q. frainetto*, *Q. robur*, *Q. petraea*, *Q. calliprinos*, *Q. canariensis*, *Q. macrolepis*, *Q. boissieri*, and *Q. coccifera*, whereas some regionally important Mediterranean taxa, such as

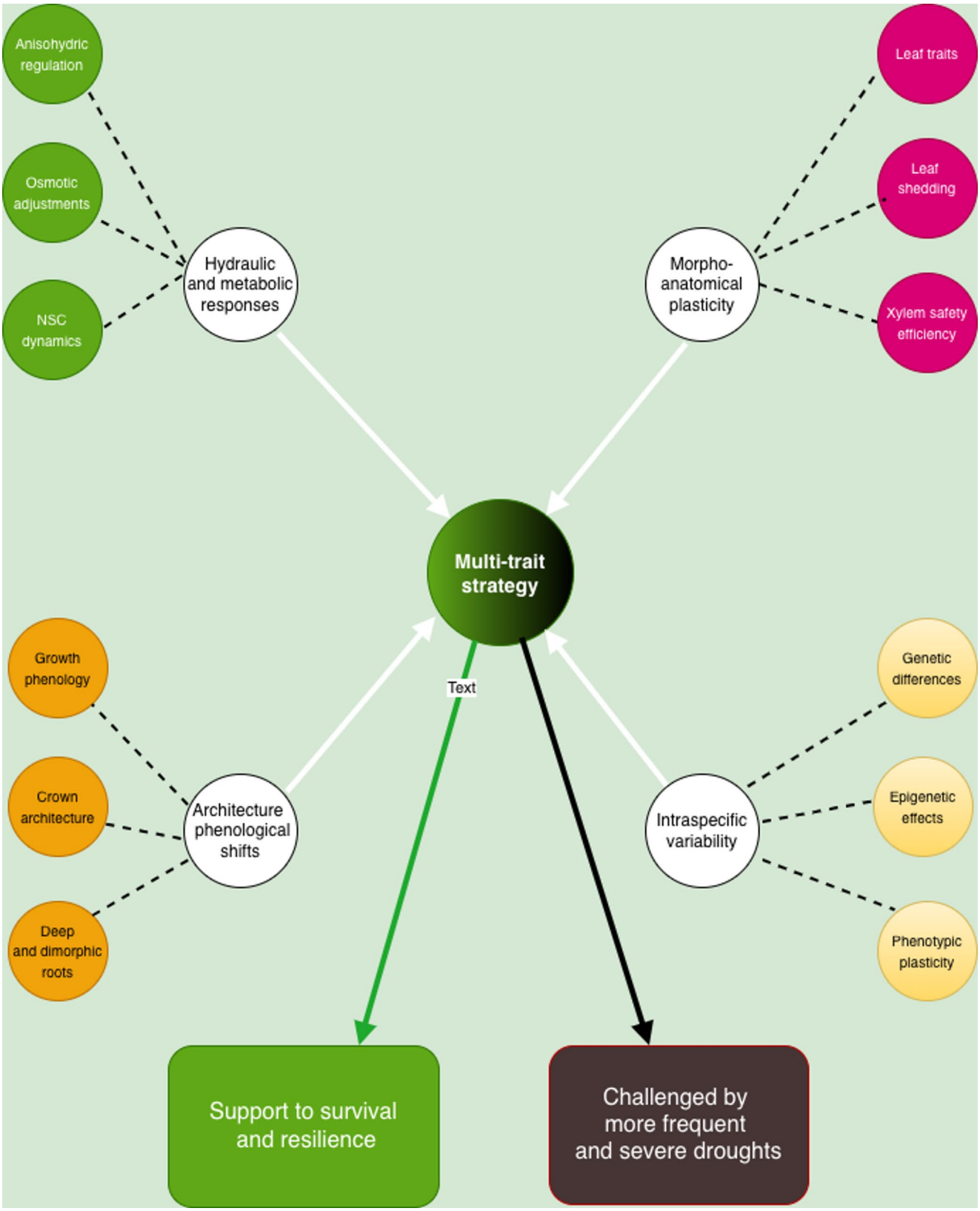

Anisohydric regulation
Osmotic adjustments
NSC dynamics
Hydraulic and metabolic responses
Leaf traits
Leaf shedding
Xylem safety efficiency
Morpho-anatomical plasticity
Multi-trait strategy
Growth phenology
Crown architecture
Deep and dimorphic roots
Architecture phenological shifts
Text
Genetic differences
Epigenetic effects
Phenotypic plasticity
Intraspecific variability
Support to survival and resilience
Challenged by more frequent and severe droughts

Fig. 1 Conceptual framework of drought-response domains in Mediterranean oaks. The diagram represents the key mechanisms described in the narrative synthesis: (i) hydraulic and metabolic regulation, (ii) morpho-anatomical plasticity, (iii) architectural and phenological shifts, and (iv) intraspecific variability. These domains converge to form coordinated multi-trait strategies that shape drought resistance and resilience. Drought regimes are characterized by both severity and frequency, which constitute distinct but interacting dimensions influencing the effectiveness of these strategies and determining whether they sustain tree and forest function or become overwhelmed, leading to elevated vulnerability

Q. trojana and *Q. ithaburensis*, are not represented in the selected studies.

Several studies contributed more than one record (e.g., representing different drought intensities, developmental stages, or response variables), so the dataset comprises a mixture of within-study and among-study contrasts. Because no explicit weighting by study or species was applied, taxa that have been more frequently studied, particularly *Q. ilex*, exert a greater influence on overall frequencies and ordination results. The dataset should therefore be regarded as a structured overview of where experimental effort has been concentrated, rather than a balanced representation of all Mediterranean oak taxa and environments.

This structure, summarized in Table 2, provides the biogeographic and functional context for all subsequent analyses of oak drought responses presented in this review. The duration and intensity of drought treatments vary widely, from short-term experiments lasting days or weeks to multi-year studies. Intensity levels predominantly encompass intermediate to severe stress conditions (Table 3), reflecting the emphasis of most experiments on ecologically relevant drought events rather than mild water limitation.

Descriptive statistics were generated in the R environment (R Core Team, 2025, version 4.5.2) to characterize the frequency of response mechanisms and categories across the dataset. Comparisons were made among functional groups defined by leaf habit and wood anatomy, as well as among taxonomic sections within the genus *Quercus*. These analyses provided an overview of drought-related variability, including the frequency of ecophysiological mechanisms, geographic patterns of resistance and resilience, and comparative differences in drought responses along gradients of plant diversity.

An unconstrained correspondence analysis (CA) was additionally performed using the 'ca' package in R on the following variables: leaf habit, wood type, taxonomic section, plant stage, ecophysiological response mechanism, effect of drought on plant function (assimilation, vigour and vitality), system resistance, system resilience (Tables 1 and 2). For each variable, a binary incidence matrix (0/1) was created, coding presence as 1 and absence as 0, following Greenacre (2000). These matrices were concatenated column-wise into a single matrix, on which CA was performed. The package reports the inertia explained by each dimension and applies an adjustment to correct for inflation caused by diagonal blocks (Greenacre 2000, p. 148). The resulting row coordinates were perfectly correlated with those obtained using other R implementations of CA (e.g., 'vegan' and 'FactoMineR'), differing only by a scaling factor.

Frequency of drought-response mechanisms

'Radar' plots provide a visual overview of the frequency with which various ecophysiological mechanisms have been studied in the context of Mediterranean oaks' drought response, thereby highlighting prevailing research trends and revealing existing knowledge gaps (Fig. 2).

Throughout the reviewed literature (Fig. 2a), regulation of stomatal aperture to limit transpiration (short-term, ST, stomatal control) and yearly and seasonal changes in stem growth due to dry periods (long-term, LT, growth patterns) consistently emerge as the most commonly investigated drought responses. These mechanisms are frequently analyzed because they exert a prominent and immediate influence on oak survival under water-limited conditions and represent some of the most readily observable consequences of drought.

Other responses, such as modifications in plant structure or shifts in biomass allocation (LT structural responses), changes in wood anatomy (including vessel size, density, or spatial arrangement, representing LT adjustments in xylem functional traits), and modifications in leaf characteristics (morphology, thickness, or chemistry; LT leaf modifications), are less frequently documented, yet they play important roles in plant adaptation and may contribute to long-term resilience. However, strategies such as leaf abscission to limit water loss (ST leaf shedding) and cellular solute accumulation to maintain turgor (ST osmotic adjustment) appear least represented in the literature, suggesting that these responses warrant further investigation given their potential functional significance.

Analysing these responses by oak functional type, defined by leaf habit and wood anatomy, reveals distinctive patterns (Fig. 2b, c). Long-term growth adjustments are more frequently reported for deciduous species, whereas evergreen species are more often investigated for structural adaptation mechanisms. Considering wood functional types, semi-ring-porous oaks show a tendency for more pronounced adjustments in wood-related traits and growth patterns, while ring-porous and diffuse-porous oaks are more commonly studied for structural adaptations. It is important to note that these differences partly reflect the over-representation of *Q. ilex* in our dataset (Table 2), which means that the

Table 1 The considered categories and scores assigned; ST: short-term; LT: long-term; IT: intermediate term; XFT: xylem functional traits

Category	Notes
Section A: plant categories, drought characteristics and assigned scores	
Leaf habit[1)]	
1: Evergreen	Leaves persist for multiple years; canopy remains green year-round
2: Deciduous	Leaves are shed all at once, typically in autumn, leaving the tree leafless in winter
3: Semi-persistent	Leaves dry but persist during part or all of the cold season until new foliage emerges
Wood type[2)]	
1: Diffuse-porous	Vessels distributed evenly throughout the annual ring
2: Ring-porous	Large early-wood vessels form a ring at the start of the growing season
3: Semi ring-porous	Vessels gradually decrease in size from earlywood to latewood, without distinct zones
Plant stage	
1: Seedling	
2: Tree	
3: Stand or forest level	
Drought duration	
1: Days or weeks	Short term (ST)
2: Months	Seasonal to intermediate-term (IT)
3: Years	Long-term or chronic drought conditions (LT)
Drought intensity	
1: Weak	modest reductions in precipitation or soil moisture, usually not causing marked declines in assimilation, vigour or vitality
2: Intermediate	moderate reductions in precipitation or soil moisture and/or intermittent drops in plant water status, typically associated with measurable but not extreme impacts on growth or physiological function
3: High	severe or prolonged water deficits, often quantified by marked precipitation anomalies, low drought indices or strong soil moisture depletion, and generally associated with substantial reductions in assimilation, growth, vigour or vitality
Section B: plant responses and assigned scores	
Ecophysiological response mechanisms investigated/observed[3)]	
1: ST stomatal control	Regulation of stomatal aperture to limit water loss
2: ST osmotic adjustment	Accumulation of solutes to maintain cell turgor
3: ST leaf shedding	Abscission of leaves to reduce transpiration
4: LT leaf modification	Adaptations in leaf size, thickness, or chemistry
5: LT structural response	Modifications to plant structure/architecture or biomass distribution
6: LT adjustments in XFT	Modifications in vessel size, density, or arrangement
7: LT growth patterns	Yearly and seasonal changes in stem growth
8: Coordinated response	Multi-trait response: integration of short- and long-term mechanisms
Effects of drought on plant function: scored for assimilation, vigor, and vitality	
0: No effect	
1: Weak	
2: Intermediate	
3: High	
System resistance[4)]	The ability of a plant system to maintain core physiological and ecological functions
1: Weak	
2: Intermediate	
3: High	
System resilience[4)]	The ability of a plant system to recover physiological function and growth after drought
1: Weak	
2: Intermediate	
3: High	

[1)] Galle et al. (2011) provide definitions and contrasts for leaf habits among Mediterranean oaks

[2)] Castagneri et al. (2020) compares these anatomical types in Mediterranean *Quercus* species

[3)] Choat et al. (2012) and McDowell et al. (2008) comprehensively describe these mechanisms

[4)] We have applied and extended the framework proposed by Lloret et al. (2011) for assessing tree resistance and resilience generalizing their growth-based definitions to categorical assessments at the plant-system level (seedlings, individual trees, and forest stands)

Table 2 Number of records (N) in the dataset corresponding to individual *Quercus* species and their assignment to sections within the genus *Quercus*, according to the phylogenetic framework proposed by Hipp et al. (2020). *Q. ilex* includes *Q. rotundifolia*, and *Q. pyrenaica* includes *Q. subpyrenaica*.The label 'Multiple species' refers to studies in which two or more of the listed oak species were considered, without the possibility of attributing the observed effects to any single species

Species *N* Section
Q. ilex 104 *Ilex*
Q. coccifera 5 *Ilex*
Q. calliprinos 5 *Ilex*
Q. pubescens 37 *Quercus*
Q. pyrenaica 8 *Quercus*
Q. faginea 8 *Quercus*
Q. frainetto 6 *Quercus*
Q. robur 2 *Quercus*
Q. petraea 2 *Quercus*
Q. canariensis 1 *Quercus*
Q. boissieri 1 *Quercus*
Q. cerris 12 *Cerris*
Q. suber 20 *Cerris*
Q. macrolepis 1 *Cerris*
Multiple species 28 -
Total 240
Section *Ilex* 114
Section *Quercus* 65
Section *Cerris* 33

Table 3 Number of records (N) in the dataset for the categories listed in Table 1, section A. Not all categories are represented in every record of the dataset

Category *N*
Leaf habit
Evergreen 137
Deciduous 27
Semi-persistent 54
Wood type
Diffuse-porous 137
Ring-porous 62
Semi ring-porous 19
Stage of the plant system
Seedling 51
Tree 138
Stand/Forest 51
Drought duration
Days/weeks 25
Months 69
Years 135
Drought intensity
Weak 7
Intermediate 46
High 160

frequency plots are more strongly influenced by this species than by less-studied taxa. Consequently, the observed gradients should be interpreted primarily as summarizing where experimental effort has been concentrated, rather than as a balanced comparison across all Mediterranean oak species.

Despite this diversity, a major gap is apparent: few studies examine coordinated responses that integrate multiple traits or processes, especially those addressing how these traits work together in real-world, multifactorial drought and stress scenarios. Integrative studies are crucial, as Mediterranean oaks are increasingly exposed to complex combinations of drought alongside other abiotic stresses. Future research should therefore prioritize mechanistic, multi-trait approaches across species and spatial scales to better predict oak resilience and guide effective adaptation strategies in the face of climate change.

Assessment of geographic structure

Potential variation in drought resistance, resilience, and ecophysiological response mechanisms across geographic gradients in the assembled dataset was explored using the subset of data in which the plant stage was represented by trees or forests/stands, thereby focusing on studies conducted in field conditions. The rationale for this analysis lies in the recognised ecological significance of environmental gradients (particularly those reflecting east–west regional differences) across the Mediterranean Basin (Matesanz and Valladares 2014). In particular, longitude may serve as a proxy for continentality, distinguishing the oceanic-influenced western Mediterranean from the more continental eastern regions (Lionello et al. 2006).

In our dataset, latitude alone does not represent an axis of variation in system resistance and resilience, as indicated by the broadly uniform boxplot distributions along the relatively modest latitudinal gradient. Although longitudinal gradients span a wider range, no distinct geographic patterns emerge in this case. With regard to altitudinal variation, higher resilience scores are apparent at lower elevations, possibly reflecting long-term adaptations of oak populations to lowland semi-arid conditions (Fig. 3). Regarding response mechanisms, no latitudinal variation is apparent, whereas mechanisms such as osmotic adjustment, xylem modification, and coordinated multi-trait responses appear more frequently in more continental eastern and upland areas (Fig. 4).

These upland and more continental sites often experience colder winters in addition to intense summer drought, suggesting that selection for combined freeze and drought tolerance may favour strategies that enhance hydraulic safety through xylem reinforcement and solute accumulation. Experimental studies along latitudinal gradients in *Q.*

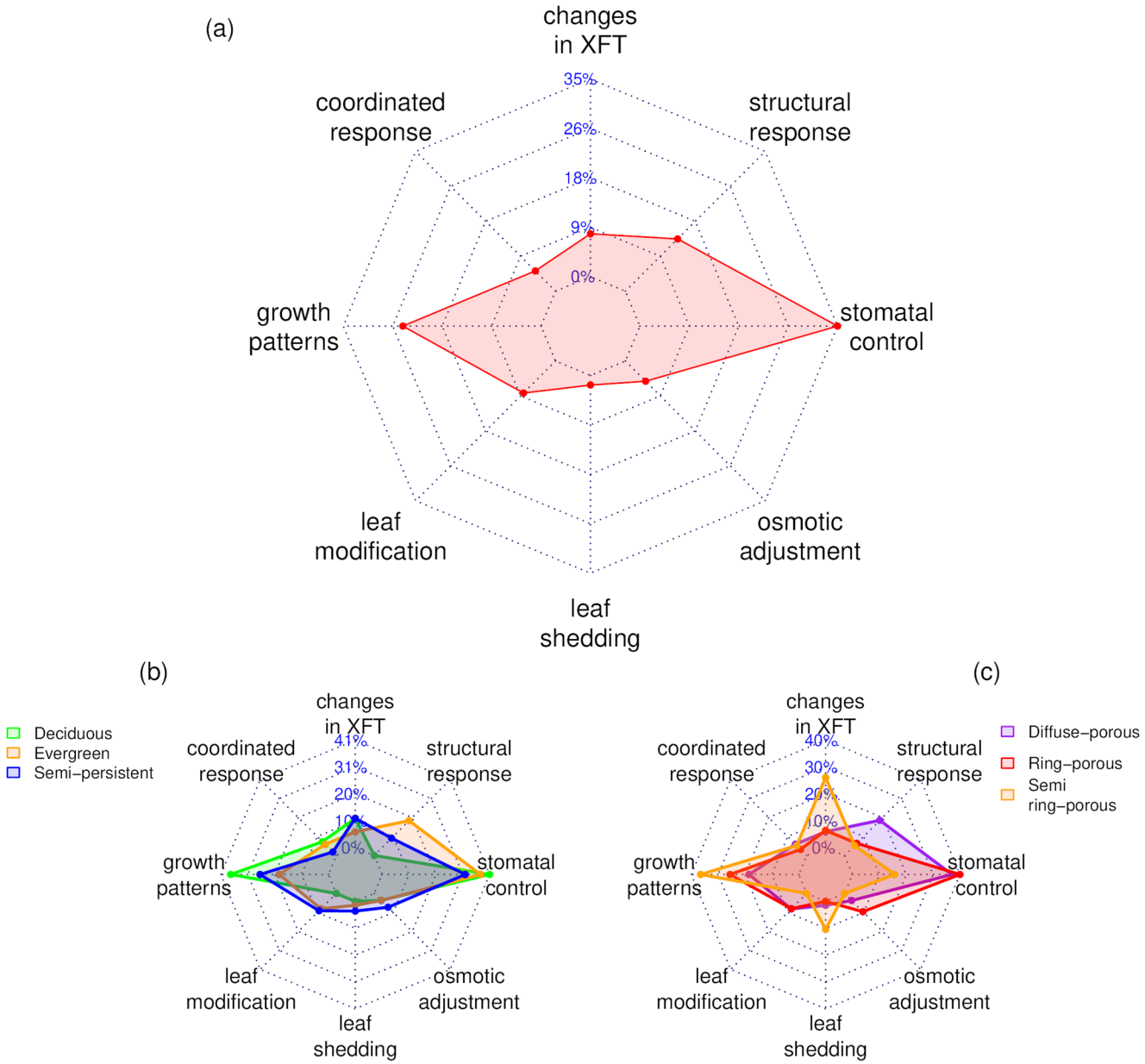


Fig. 2 Frequencies of drought-response mechanisms across Mediterranean oak studies. Radar plots illustrating the relative representation of short- and long-term response mechanisms in the 212-study dataset: (**a**) the entire dataset; (**b**) contrasts among leaf habits (evergreen, deciduous, semi-persistent); and (**c**) contrasts among wood anatomical types (diffuse-porous, ring-porous, semi-ring-porous). XFT: xylem functional traits

ilex and other oaks indeed show that populations exposed to both low temperatures and summer aridity adjust their embolism resistance and tissue sclerophylly, highlighting the need to integrate multiple stress axes when interpreting geographic patterns of response mechanisms (Nardini et al. 2000; Mazza et al. 2024).

The lack of a clear geographic pattern in our categorical scores should not be taken as evidence of spatial homogeneity. Instead, it likely reflects the combined effects of coarse response classes, uneven species representation, and heterogeneous experimental designs, which can obscure the finer-scale climatic signals documented in dendroecological studies (Tumajer et al. 2022). These limitations also likely impede the detection of the full range of trait plasticity and adaptive potential stemming from the evolutionary history and genetic variability of Mediterranean oak species (Kremer and Hipp 2020; Pütz et al. 2025).

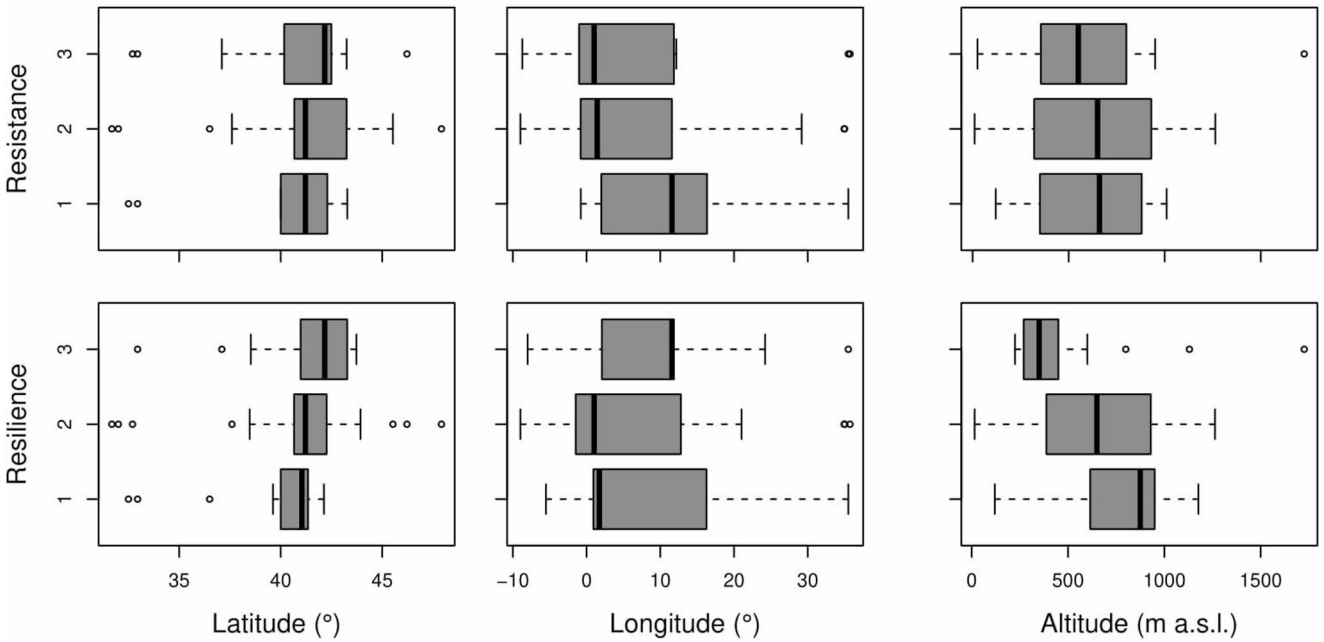


Fig. 3 Boxplots showing how categorical resistance and resilience scores (1 = weak; 2 = intermediate; 3 = high) vary along latitude, longitude, and elevation. Each box represents the interquartile range and median of the categorical scores. No clear latitudinal or longitudinal trends emerge, and the boxplots highlight relative tendencies in categorical resistance and resilience scores across these gradients, without implying statistically tested differences

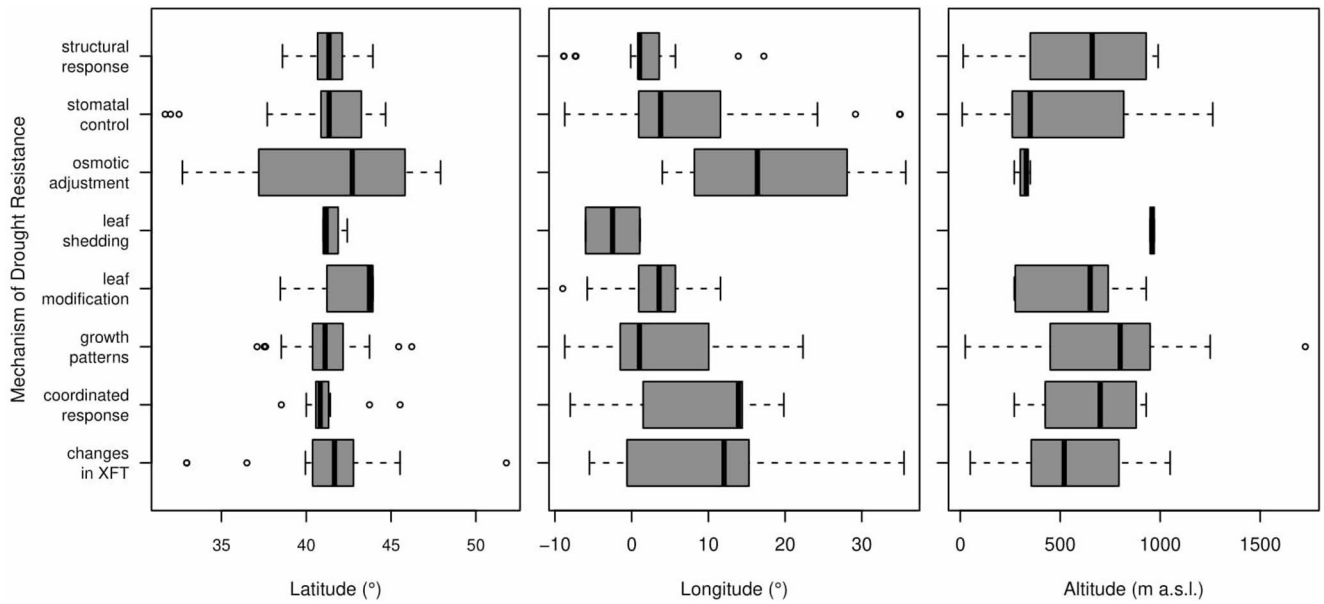


Fig. 4 Boxplots illustrating the incidence of response mechanisms as a function of latitude, longitude, and elevation. Each box represents the interquartile range and median of the categorical scores

Drought resistance and recovery across functional types

Patterns of drought resistance and resilience, as illustrated in the comparative histograms (Figs. 5 and 6), appear to be modulated by plant diversity. For instance, when the frequency of 'weak resistance' and 'weak resilience' scores is considered as a proxy for elevated drought vulnerability, subtle yet consistent gradients emerge across leaf habit, wood anatomy, developmental stage, and taxonomic sections, which merit consideration.

Deciduous oaks tend to appear more vulnerable to drought and less effective at recovering under recurrent or severe drought conditions than their semi-persistent and

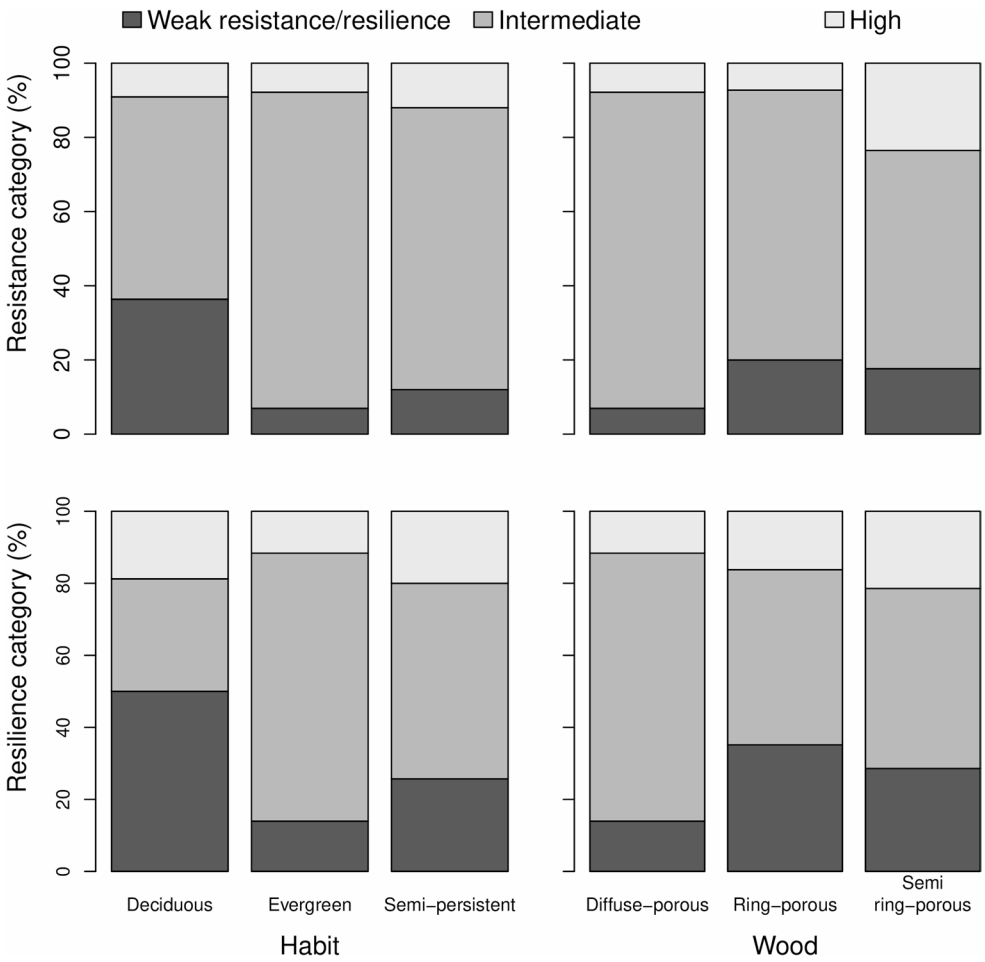


Fig. 5 Drought resistance and resilience across leaf habits and wood anatomical types. Stacked histograms show the frequency distribution of resistance and resilience categories for (left) leaf habits and (right) wood types.Associations between drought response categories and functional groups were tested using Fisher's exact test on contingency tables, evaluating the null hypothesis of independence. Significant differences were detected among leaf-habit categories for resistance ($p=0.005$) and resilience ($p=0.015$), and among wood-type categories for resistance ($p=0.015$) and resilience ($p=0.004$)

evergreen counterparts. Such differences may arise from the distinct strategies that oaks with varying leaf habits employ to maintain hydraulic safety margins, which are critical in determining susceptibility to hydraulic failure during periods of water stress (Moreno et al. 2024). This observation accords with projections that suggest a reduced competitive capacity for deciduous species within the supra-Mediterranean vegetation zone. The interplay between drought intensity, plant physiological traits, and the broader shifts anticipated under ongoing climate change may disadvantage deciduous taxa relative to their evergreen counterparts in these environments (Serrano and Peñuelas 2005).

Wood anatomy constitutes a second axis of variation, with ring-porous oaks demonstrating the greatest drought vulnerability. This finding can be attributed to their dependence on large earlywood vessels, which are especially susceptible to embolism during periods of substantial water deficit. Tree-ring records often indicate that drought legacies are particularly pronounced in ring-porous taxa, with multi-year growth depressions following severe events (Bose et al. 2024), potentially contributing to the higher frequencies of low-resistance and low-resilience states inferred here. Semi-ring-porous types exhibit an intermediate response, whereas diffuse-porous species, which invest in narrower vessels and denser wood, show the lowest frequencies of 'no resistance' and 'no resilience' states. This trend reflects their broader hydraulic safety margins and greater acclimation capacity (Serrano and Peñuelas 2005; González de Andrés et al. 2021). Notably, these anatomical differences largely parallel those documented for leaf habit in the preceding discussion, as ring-porous xylem is typical of most deciduous species.

It has been reported that drought increases mortality risk in juvenile plants and cohorts, and that prolonged legacy effects can reduce ecosystem-level recovery and promote forest replacement after drought-related dieback (Batlori et al. 2020; Serra-Maluquer et al. 2025). Evidence also suggests that oak species in the *Quercus* section are more prone to drought-induced losses of resistance and resilience than those in the *Cerris* and *Ilex* sections, and may need to rely more heavily on intraspecific variability and admixture. However, in the dataset analysed here, the frequencies of resistance and resilience did not differ significantly between plant stages or among taxonomic sections (Fig. 6), indicating that these patterns were not detectable using the coarse categorical metrics employed.

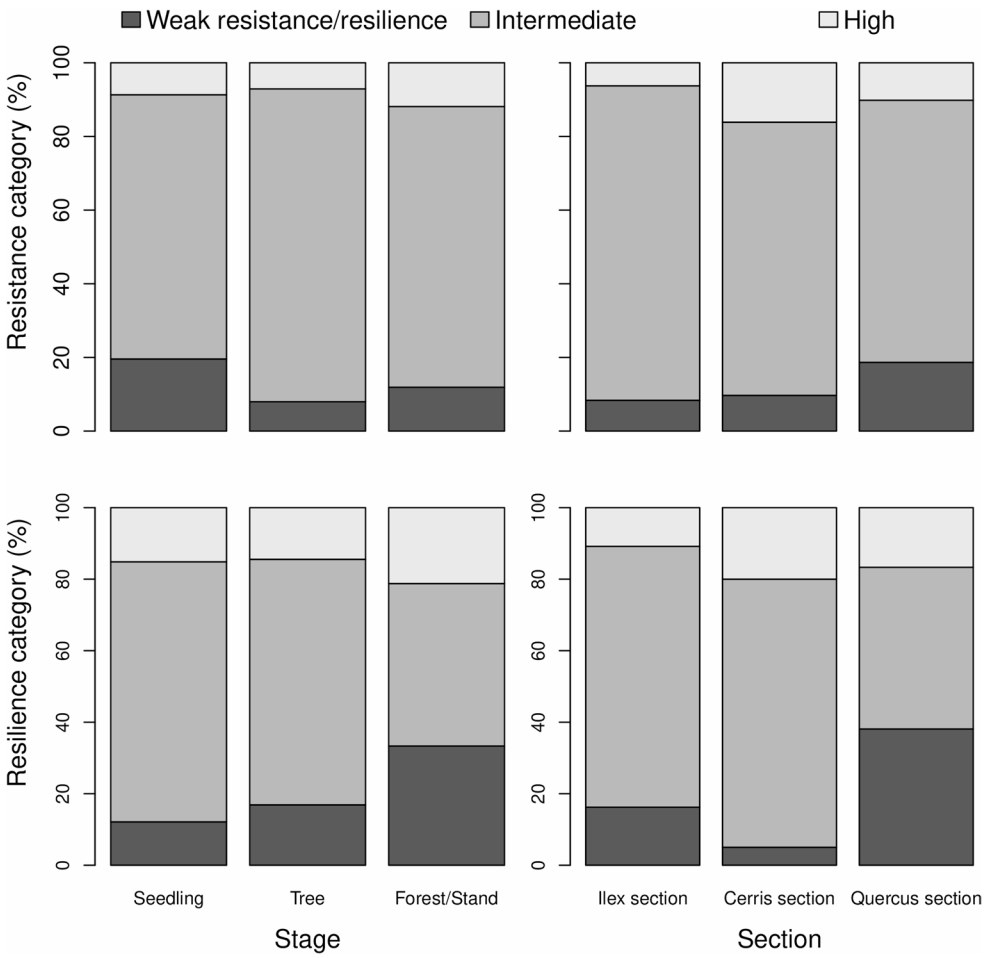


Fig. 6 Drought resistance and resilience across plant developmental stages and taxonomic sections. Stacked histograms show the frequency distribution of resistance and resilience categories across developmental stages (seedlings, trees, stands) and *Quercus* taxonomic sections. Associations were tested using Fisher's exact test on contingency tables, and no significant differences were detected among developmental stages or taxonomic sections

Similarly, in several studies contributing to low-resistance and low-resilience records, droughts were classified as high intensity; however, categorical scoring and uneven sampling across intensity classes preclude the detection of a simple quantitative gradient.

Functional axes of oak drought response

Correspondence analysis (CA) of the assembled categorical dataset reveals clear ecological differentiation among oak species when categorised by leaf habit and wood anatomical type (Fig. 7).

We acknowledge that, because leaf habit and wood anatomy were included among the input variables, their separation should not be interpreted as an independent test of their effects. However, these variables exert the strongest influence – more than any others – on the two major axes that structure the broader multivariate patterns of drought responses in our dataset.

The first two axes account for 59.8% of the total inertia. In Fig. 7, three distinct groups of observations can be identified, corresponding to the three leaf-habit types. The first axis, which explains 45.6% of the total inertia, differentiates evergreen plants from the other two groups, whereas the second axis, accounting for 14.2%, separates deciduous plants from semi-persistent ones.

The first principal axis is primarily associated with evergreen and semi-persistent habits, semi-ring-porous wood, while the second axis is most strongly influenced by a deciduous habit. Variables related to developmental stage, resistance, and resilience do not appear to play a role in this ordination, although some drought resistance mechanisms – particularly leaf modification and leaf shedding – show a weak association with the first principal axis. Both axes also show modest correlations with geographic variables, suggesting that the pattern in Fig. 7 is partially influenced by the spatial distribution of sampling locations. The first principal axis was positively correlated with latitude (r = -0.208, df = 107, p = 0.03) and longitude (r = -0.209, df = 107, p = 0.029).

The pronounced differentiation by wood anatomical type underscores the critical role of functional hydraulic traits in determining both drought vulnerability and recovery potential, as documented for related Mediterranean tree taxa. Xylem functional traits and wood characteristics – such as conduit size, wood density, and hydraulic conductivity – are

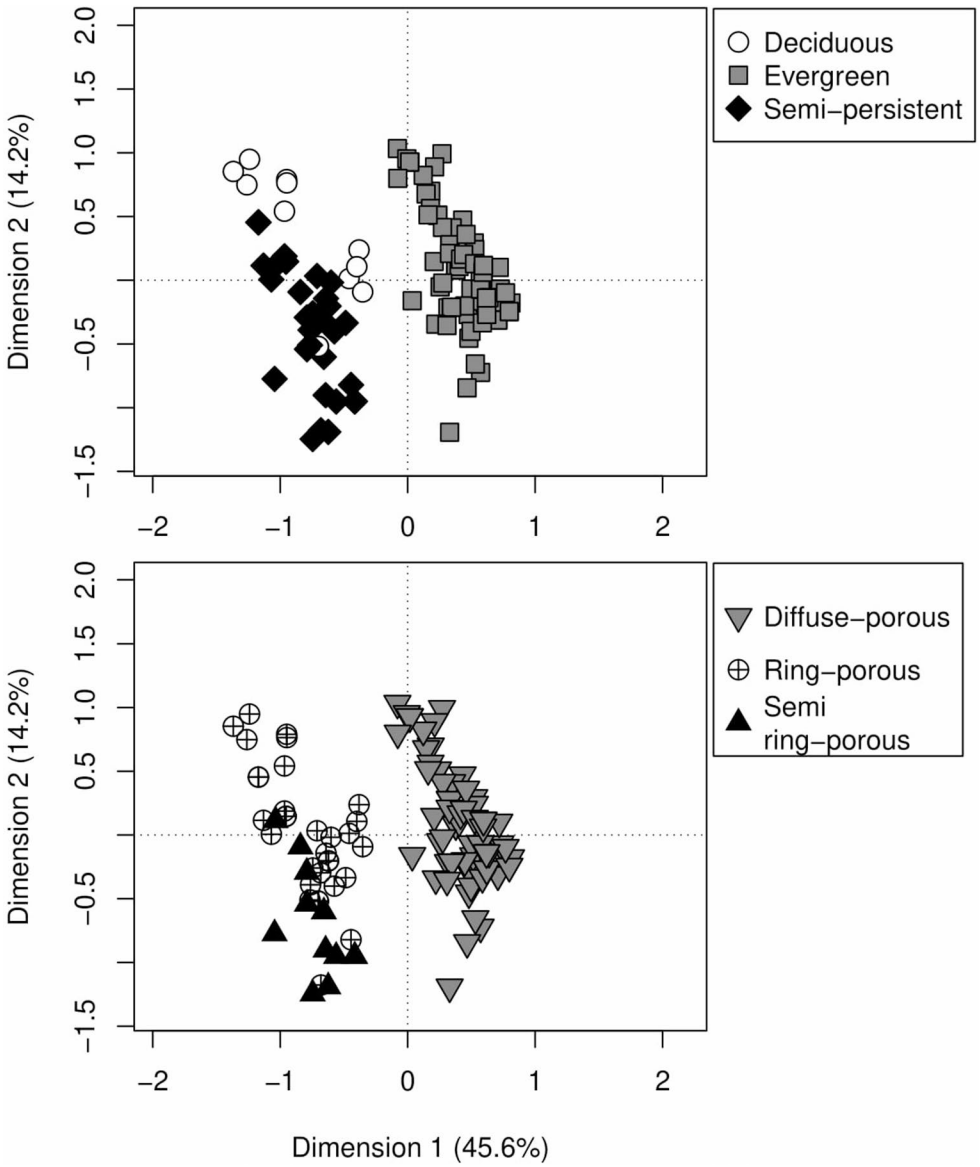


Fig. 7 Correspondence analysis ordination of all records in the categorical dataset, classified by leaf habit and wood anatomy

valuable indicators for interpreting forest properties, defining species distribution limits, and understanding climate-driven changes in forest vegetation Alonso-Forn et al. 2021; Campelo et al. 2023; Colangelo et al. 2025).

These results indicate that the main functional types follow distinct ecophysiological trajectories, and the ordination supports the existence of contrasting adaptive models among Mediterranean oaks under drought. Notably, evergreen oaks tend to rely on strict regulation of water use combined with reinforced xylem structures, whereas deciduous and semi-persistent species are more strongly associated with phenological plasticity and flexible leaf development.

Taken together, the observed gradient from evergreen, diffuse-porous to deciduous, ring-porous oaks indicates that functional types, rather than individual species, offer a practical framework for anticipating community shifts and guiding management decisions under intensifying drought regimes. Furthermore, the functional axes identified through correspondence analysis provide a basis for stratifying monitoring networks, designing multi-site common-garden experiments, and parameterizing trait-based models of forest vulnerability to recurrent drought.

Conclusions

Mediterranean oaks display a diverse suite of drought-adaptation mechanisms that collectively support their persistence under increasingly arid and variable climates. However, current evidence reveals an uneven and only partially integrated understanding of these responses.

Key insights from the literature synthesis and from the analysis of the categorical dataset include: (i) Mediterranean oaks employ a combination of hydraulic regulation, osmotic adjustment, anatomical modification, and phenological plasticity, yet most studies examine these mechanisms in isolation rather than as components of coordinated multi-trait response. Research has focused predominantly on short-term stomatal regulation and long-term growth responses, with comparatively fewer studies addressing structural adjustments, xylem functional traits, osmotic regulation, or leaf-level morphological acclimation; (ii) drought resistance and resilience appear structured along gradients of functional diversity, particularly leaf habit and wood anatomy. Evergreen, diffuse-porous species generally exhibit larger hydraulic safety margins and fewer low-resistance, low-resilience states than deciduous, ring-porous species, while semi-persistent and semi-ring-porous types show intermediate responses; (iii) the gradient from evergreen, diffuse-porous to deciduous, ring-porous oaks shows that functional types, rather than individual species, provide a practical framework for anticipating community shifts. The functional axes identified through correspondence analysis further support monitoring design, multi-site experiments, and trait-based modeling of forest vulnerability to recurrent drought.

From a management perspective, these contrasts support strategies that promote structurally diverse, mixed stands and reduce stress on drought-sensitive deciduous and ring-porous taxa, especially in supra-Mediterranean belts, through targeted thinning, regeneration planning, and species selection in restoration efforts.

Future research should prioritize: (i) quantifying coordinated multi-trait responses across hydraulic, carbon, structural, and phenological dimensions; (ii) linking ecophysiology, dendroecology, functional anatomy, and remote sensing across organizational scales; (iii) disentangling local adaptation from phenotypic plasticity through multi-site and common-garden experiments; and (iv) incorporating leaf habit and wood anatomy into trait-based projections of forest stability and productivity under increasingly frequent and severe drought.

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Author contributions M.B.: conceptualization, methodology, manuscript writing, and supervision; M.C.: methodology, dataset construction; S.L.: methodology, data analysis, and manuscript review.

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Declarations

Conflict of interest Marco Borghetti, Maria Castellaneta and Stefano Leonardi declare they have no conflict of interest.

Human and animal right and informed consent This article does not contain any studies with human and animal subjects performed by any of the authors.

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