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Distinct Functioning of Low- Versus High-Altitude Refugia in the Mediterranean: Inferences From Life-History Traits of Two Related Relict Trees From the Islands of Sicily and Crete

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ABSTRACT

Aim: Relict trees are the outcome of long-term 'natural experiments'. Accordingly, they provide opportunities to study the effects of local adaptation of trees, which are still poorly understood but crucial in the context of climate change. In turn, the physical settings of refugia at macro- and microscale are the key drivers of the environmental adaptability of such species. Using two congeneric climate relict trees (*Zelkova sicula* and *Z. abelicea*) as model species, we analysed the functional relationships between tree growth patterns and the distinctive environmental drivers of low- versus high-altitude refugia in the Mediterranean.

Location: Mediterranean islands of Sicily (Italy) and Crete (Greece).

Methods: To evaluate the growth potential of the two relict trees we used top height and multi-year data of shoot length over the entire distribution range of both species. Growth form and height growth dynamics of *Z. sicula* were also investigated by stem analysis. Moreover, tree-ring response to climate was compared through classical dendrochronological approaches.

Results: Tree size, as well as shoot and radial growth are notably greater in *Z. abelicea*, suggesting this species better fits in its habitat and the higher-elevation Cretan refugia are less constraining than their low-elevation Sicilian counterparts. Tree-ring growth response to precipitation and evapotranspiration is rather similar between the two species and points to the key role of moisture balance on growth. However, the 1-month delay in the response from the Sicilian to the Cretan relict mirrors the differential role of altitude against micro-topography in decoupling from the regional climate.

Main Conclusions: The significant attenuation of environmental constraints due to the 'elevation effect' is a major offsetting driver for the distinct functioning of low- versus high-altitude refugia in the Mediterranean, but macroclimatic patterns may locally blur the effectiveness of refugia in a long-term conservation perspective.

1 | Introduction

Climate relict species are organisms that were once widespread over broad regions of the globe but experienced changing and adverse environmental conditions that caused their extinction over large parts of their range (Hampe and Jump 2011). Relicts persist only in large-scale climatic refugia (Dobrowski 2010) or in restricted refugial sites in which local microenvironmental conditions are decoupled from the regional climate, allowing the species to survive (Rull 2009, 2010; Hampe and Jump 2011). In particular, the warm and humid climate that prevailed during the Paleogene gradually began to cool at the beginning of the Oligocene, shifting from greenhouse to icehouse conditions (Speijer et al. 2020). The species that were not able to tolerate colder and drier climates or migrate or survive in refugia experienced fragmentation of their range or even extinction. Therefore, current relict species have high biogeographical and conservation value because they are the only surviving members of taxa with a complex evolutionary history (Woolbright et al. 2014), and at present, they are also often extremely rare and/or spatially localised (Grandcolas, Nattier, and Trewick 2014; Garfì et al. 2021). Moreover, as a result of long-term 'natural experiments', climate relicts provide opportunities to study the effects of local adaptation and evolutionary processes, which still remain poorly understood but are crucial to comprehend in the current context of climate change (Hampe and Jump 2011; Woolbright et al. 2014; Ackerly et al. 2020).

The relict plants that persisted the longest or survived in Southern Europe during the Quaternary glaciations are relatively thermophilic and drought tolerant (Svenning 2003); alternatively, these are species that developed local adaptations resulting from long isolation in microrefugia (Mee and Moore 2013), or even taxa originating from 'ecological' speciation under strong adaptive selection in marginal habitats (Stewart et al. 2010; Nieto Feliner 2011; Kiedrzyński et al. 2017). The Mediterranean region did not fully escape major (or rapid) climatic fluctuations (Milne and Abbott 2002), but the diffuse presence of large islands and peninsular areas resulted in the existence of macro- and microscale refugia (Médail and Diadema 2009) for many Cenozoic relict plants by offering them a variety of suitable habitats where climatic conditions were warmer and moister than elsewhere. Furthermore, this region not only provided conditions that prevented species extinction but also favoured speciation by putting species into contact and allowing hybridization (Médail and Diadema 2009). Therefore, the endurance of single taxa in this area results from processes that should be analysed from both an ecological and an evolutionary perspective. In turn, the physical settings of refugia at both the macro- and microscales should be regarded as key drivers of the environmental adaptability and fitness of such species.

The broad-leaved deciduous tree genus *Zelkova* (Ulmaceae) is one of such relict taxa, whose ancestors were widespread across the Northern Hemisphere at the beginning of the Cenozoic. The members of this genus underwent a massive distribution retreat due to the changing climatic conditions of the late Paleogene until they acquired their current and extremely fragmented and disjunct range (Kozlowski, Gibbs et al. 2012). The genus currently includes six extant species, three of which occur in Southeast Asia, namely, *Zelkova sinica* C.K. Schneid., *Z. serrata* (Thun.) Makino and *Z. schneideriana* Hand.-Mazz., one lives only in the Transcaucasian region, *Z. carpinifolia* (Pall.) K. Koch, and the last two are endemic to the Mediterranean islands of Crete, Greece (*Z. abelicea* (Lam.) Boiss.) and Sicily, Italy (*Z. sicula* Di Pasq., Garfì & Quézel). Within the genus, all but one species are considered globally threatened according to the IUCN Red List criteria, with the two Mediterranean insular taxa ranked at the highest risk levels (EN and CR, respectively; see Kozlowski, Frey et al. 2012; Garfì et al. 2017).

The two Mediterranean relicts share several morphological or physiological adaptations to the summer drought typical of the Mediterranean climate (Wang et al. 2001; Denk and Grimm 2005; Garfì et al. 2021; Jasińska et al. 2022), which clearly distinguish them from the Transcaucasian and eastern Asian *Zelkova* species (Fragnière et al. 2021). However, they differ remarkably from one another in terms of their geographic and altitudinal range as well as their growth habits and genetic patterns (Christe et al. 2014). *Z. sicula* is confined to two small sites in southeastern Sicily. Fewer than 2000 individuals are distributed over a very restricted area (less than two hectares), below 530 m a.s.l., along ephemeral seasonal streams (see Garfì et al. 2011, 2021). This species is the only triploid and sterile one within the genus (Fineschi et al. 2004; Christe et al. 2014), and each population is composed of a unique clone, with individuals typically growing as small/dwarf shrubs (Garfì et al. 2011, 2017). *Z. abelicea* includes more than 1,000,000 estimated individuals (Kozlowski et al. 2014) found in scattered subpopulations ranging from a few to several thousand hectares and dispersed throughout the main mountain ranges of Crete (Kozlowski et al. 2014, 2018; Fazan et al. 2021). It typically grows on north-facing stony slopes up to approximately 1600 m a.s.l. Egli (1997); Søndergaard and Egli (2006); Fazan et al. (2017). The species has high genetic diversity within and among populations, with between-mountain structuring (Fineschi et al. 2004; Christe et al. 2014). Although scattered stands composed of large trees occur in the Levka Ori (W Crete), a dwarfed and shrubby growth form largely prevails, increasing in abundance along a west–east gradient (Kozlowski et al. 2014; Goedecke and Bergmeier 2018).

All sites allowing the survival of the two Mediterranean relicts, both in Crete and Sicily, should be considered as refugial areas. However, the flagrant differences in distribution range and tree growth form of the two trees suggest that such refugia diverge in some features and functioning mechanisms at different topographic and/or geographical scales, even assuming characters of marginality with respect to the possible

optimum for the target species. Moreover, considering the close taxonomic affinity, the sharing of the same biogeographical region and the similarity of evolutionary history, the two Mediterranean climate relicts are pretty suitable to serve as model trees in comparative analysis of their fitness with respect to the current habitat. Therefore, the goals of this study were (1) to analyse the growth response of the two relicts to the environment throughout their entire range, using the growth attributes as indicators of the presumably different functioning of their refugia and (2) to assess the possible (micro)climatic compensation drivers among their refugial areas and the extent to which they can eventually reflect the diverse adaptations of the two species to the environmental features shaping their respective refugia.

2 | Materials and Methods

2.1 | Species Habitat Outline

Both of the investigated *Zelkova* species grow under typical Mediterranean-type climatic conditions characterised by a strong seasonality of the precipitation regime. Although both species are located at similar latitudes (*Z. sicula* at approximately 37°18′ N and *Z. abelicea* at 35°07′ to 35°34′ N), the different longitudinal position within the Mediterranean Basin and the orographic complexity in the distribution range of the two relicts results in notable differences in their respective habitats. *Z. abelicea* shows a fragmented distribution throughout the main mountain ranges (Levka Ori, Kedros, Psiloritis, Dikti and Thripti) of Crete (Figure 1) and grows from 800 to over 1600 m a.s.l. at the bottom of or near karstic dolines and poljes, along thalwegs, or on scree slopes, most often facing north. Along the upper limit of its elevation range, stands of this species can also be found on south-facing slopes (Kozlowski et al. 2018; Fazan et al. 2021). In contrast, *Z. sicula* consists of only two tiny populations, located only 17 km apart on the eastern slopes of the Iblei Mts. (southeastern Sicily) between 318 and 526 m a.s.l., mainly within more or less incised gullies (Garfì et al. 2011). Accordingly, the annual rainfall strongly varies between the habitats of the two species. The annual precipitation in the vicinity of the Sicilian populations does not exceed 800 mm (most years < 700 mm), whereas the rainiest sites in which *Z. abelicea* grows receive up to 1500 mm of rain annually, but with a significant decreasing trend from west to east, where rainfall can be reduced to approximately half (Varouchakis et al. 2018). Moreover, on the Cretan mountains, snowfall is common, and above 1400 m a.s.l. may persist
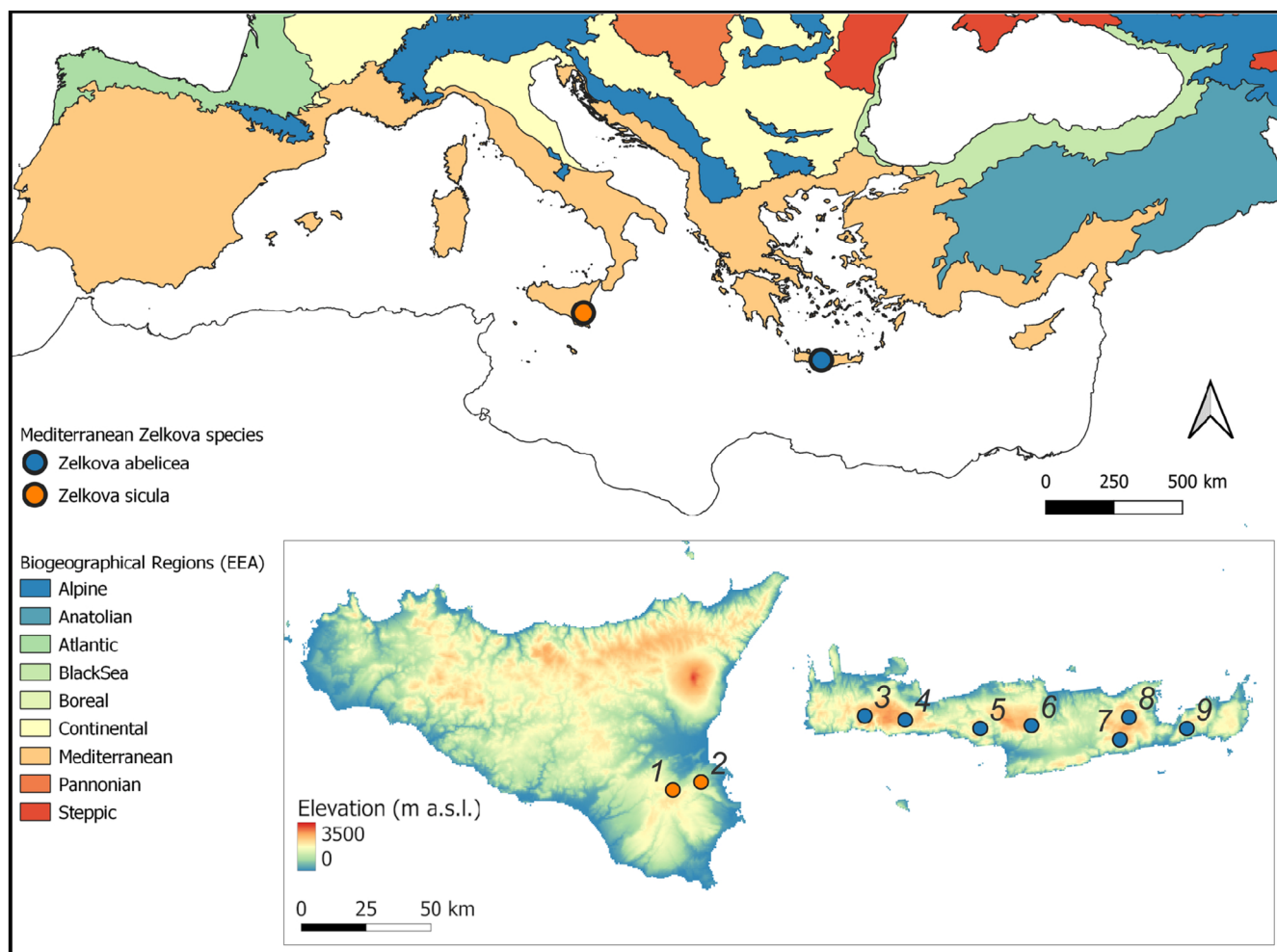
FIGURE 1 | Location of the study sites. The investigated populations are as follows. *Zelkova sicula*: (1) Pisano, (2) Ciranna (bottom and slope); *Zelkova abelicea*, (3) Levka Ori West, (4) Levka Ori East, (5) Kedros, (6) Psiloritis, (7) Dikti South, (8) Dikti North, (9) Thripti.

until May (Goedecke and Bergmeier 2018; Fazan et al. 2022). Similarly, the mean annual temperature shows considerable divergence and is usually above 16.5°C for *Z. sicula* but remains at approximately 12.0°C–13.0°C for *Z. abelicea* Fazan et al. (2017).

According to the bioclimatic classification system of Rivas-Martinez (1996), the Sicilian species lives in the thermo(−meso)-Mediterranean belt, while the Cretan species occurs in the supra- and oro-Mediterranean belts. Both species take part in a patchy mosaic of open woodlands, but the Sicilian populations mostly co-occur with *Quercus suber* L., *Olea europaea* L. var. *sylvestris* (Mill.) Lehr. and *Quercus pubescens* Willd. (Garfì et al. 2011), whereas the Cretan populations most commonly grow with *Acer sempervirens* L., *Quercus coccifera* L. and, occasionally, *Cupressus sempervirens* L. (Goedecke and Bergmeier 2018).

Although outcropping lithotypes differ between the two regions (Plio-Pleistocene basalts, in Sicily, and hard Triassic metamorphic limestones, in Crete), the soils issuing from these mother rocks share a similarly high amount of clay (Fierotti 1988; Fazan et al. 2022).

2.2 | Data Sources

To compare the differences in growth performance between the two Mediterranean *Zelkova* species within their respective distribution ranges, two basic biometric attributes were considered, namely, the height growth and the shoot length (SL). As detailed below, the data related to these two metrics originate from diverse sources (Table S1): in part, they come from original field sampling, and in part from published data, which were re-evaluated for the scope of the present investigation.

The investigated populations cover the entire distribution range of the two species and are distinguished as follows (Figure 1): for *Z. abelicea*, Levka Ori west and east (hereinafter ZA_LEV_W and ZA_LEV_E), Mt. Kedros (ZA_KED), Psiloritis Mts. (ZA_PSI, data unavailable for SL, cf. Fazan et al. 2021), Dikti Mts. south and north (ZA_DIK_S and ZA_DIK_N), and Thripti Mts. (ZA_THR); for *Z. sicula*, Bosco Pisano (ZS_PIS), and Contrada Ciranna, treating separately (cf. Garfì et al. 2021) the stands growing within the bottom of the gully (ZS_CIR1) and those located on the slope above (ZS_CIR2).

Moreover, based on a classical dendrochronological approach, a comparison of the radial growth response to climate between the two species was also carried out using unpublished (*Z. sicula*) and published (*Z. abelicea*) data (Table S1).

2.3 | Growth Form and Height Growth Dynamics

Tree growth form (*sensu* Hallé, Oldeman, and Tomlison 1978) may result from either endogenous characteristics typical of a species or from local environmental constraints that prevent a species from exceeding a given growth threshold. It is well

depicted by height, and in particular the stand dominant height or top height (TH) is often used as a common indicator of the potential site productivity or site quality (e.g., Vanclay 1992; Zhou et al. 2019; Riofrío et al. 2023). In view of the basic criteria usually considered to determine the TH (Rennolls 1978; Vanclay 1992), as well as the uneven-aged-type structure and the irregular spatial patterns of the two investigated species (Fazan et al. 2012; Kozlowski et al. 2014; Garfì, Barbero, and Tessier 2002; Garfì et al. 2011, 2021), the average height of the five tallest trees for each stand was used to calculate the TH (Table S2). The *Z. abelicea* tree size data were obtained from previous papers, whose goals already involved selecting trees among the largest ones within the investigated stands (Fazan et al. 2012, 2022; re-evaluated). These data were recorded from sampling sessions that took place between 2010 and 2017 all over Crete within the distribution range of the species, although the majority of measurements were taken in western Crete (Levka Ori). The *Z. sicula* size data were obtained and re-evaluated from Garfì et al. (2021).

Additionally, data on the actual growth potential and growth dynamics of *Z. sicula* were supplemented by a comparative analysis of the height growth-to-age relationships between 13 wild individuals over a period of 16–28 years and 1 cultivated tree over a 29-year span (Table S3). Records of the 13 wild trees concern the sole population of ZS_PIS and were obtained from a previous investigation (Garfì, Barbero, and Tessier 2002, re-evaluated) focused on the species architecture and growth patterns. The stem analysis approach was used to construct 13 individual growth-to-age curves over their entire lifespan (for methodological details, cf. Garfì, Barbero, and Tessier 2002). The cultivated tree grows since 1992 in a private garden, located in a less constraining environment at an elevation that is 325 m higher than the current highest wild population. To construct the height growth curve, measurements have been taken yearly since the plantlet stage, from 1992 to 2019.

As all populations of both species were (and on Crete still are) affected by heavy grazing (goats and sheep for *Z. abelicea*, and cows for *Z. sicula*) (Fazan et al. 2021; Garfì, Barbero, and Tessier 2002), to prevent for possible biases concerning the actual tree growth potential, reiterated measurements of SL were also carried out yearly on permanent plots that had previously been fenced to protect from browsing. The maximum SL was recorded for the same individuals for four consecutive years from 2013 to 2016 for *Z. sicula* (unpublished) and between 2015 and 2021, depending on the site, for *Z. abelicea* (Fazan et al. 2021, 2022, re-evaluated) (Table S4). The sampling procedure for the two species is explained in Garfì et al. (2021) and Fazan et al. (2021), respectively. Comparative analyses were based on the average of maximum SL for the two species.

Statistical data were computed using R version 4.2.3. (R Core Team 2023). Pairwise Wilcoxon rank sum tests with continuity correction (pairwise.wilcox.test, package stats, R Core Team 2023) were performed to assess differences in (TH) and mean annual growth between populations of the two *Zelkova* species. Differences at the species level were also evaluated through the Kruskal–Wallis rank sum test (Kruskal.test, package stats, R Core Team 2023).

2.4 | Tree Sampling for Dendrochronological Analysis

In dendrochronological studies, to maximise the climatic signal recorded in the annual ring sequences, several requirements must be met in tree selection, namely, (i) homogeneity of ecological and floristic characteristics within each population (Schweingruber 1988), (ii) low population density to reduce competition effects, (iii) minimal biotic and abiotic disturbances (Fritts 1976), (iv) dominant position of the sampled trees, (v) apparent maximum age based on the visible features of individuals (trunk diameter, crown shape) and (vi) age homogeneity within the same population. In the case of *Z. sicula*, it was quite difficult to fulfil all the above-listed criteria. At the time of sampling (December 1993), the species was known only from a single population, ZS_PIS, and the selection of individuals was influenced by several factors. As a shrub, the small diameter of the stems did not allow core sampling with the classical Pressler's increment borer; it was necessary to use a complete disc taken at the base of the stems. However, given the extreme rarity of the species (in total approximately 200 known individuals worldwide in 1993), it was unfeasible to use destructive methods. It was therefore decided to sample mostly decayed individuals who were assumed to have died during a severe drought event in the previous summer. However, to correctly date the year of death and perform accurate cross-dating among all samples, we also included a few living individuals. A total of 13 disc samples from 9 dead and 4 living individuals were collected, taking into account the standards described above as much as possible. In addition, two small cores were taken at the base of the only living tree large enough (diameter 9.8 cm) to allow coring with a 3 mm diameter borer (Table S5). Material preparation and data analyses for *Z. sicula* are described in detail in Annex 1.

For *Z. abelicea*, tree-ring data were collected in 2012. As large trees were available, the sampling strategy and material preparation were consistent with standard dendrochronological procedures, while the data analysis was almost the same as that for the Sicilian species. Major differences concerned the type of climatic data used (gridded data against real recordings) and the period of analysis (1913–2012). For a detailed description of the methodology used for *Z. abelicea*, refer to Fazan et al. (2017).

3 | Results

### 3.1 | Tree Size and Growth Dynamics

The average tree size of *Z. abelicea* was almost twofold that of *Z. sicula*, with a mean (TH) of 7.3 m for the former and 4.1 m for the latter (Table 1). However, outliers exceeding even 14 m were not infrequent within the Cretan species. At the stand level, within *Z. abelicea*, the tree size reached the highest values in Levka Ori in the westernmost sector of the distribution range. The TH herein was significantly different ($p < 0.05$) from that of all the other stands, except for those in ZA_LEV_E (Figure 2). There were no marked differences among the four populations from central-eastern Crete (Kedros, Psiloritis and Dikti Mts.); however, all of them exhibited much greater growth compared to the easternmost stand of Thripti (ZA_THR). Furthermore, the trees from these four localities were comparable in size to the Sicilian population growing in the valley bottom (ZS_CIR1). Trees from this location, in turn, grew taller than those in the two other stands of *Z. sicula*, though the difference was not significant.

The comparison between the growth dynamics of wild and cultivated *Z. sicula* trees provided additional insight into the growth

TABLE 1 | Main growth data of the investigated species and populations.

Species	Site	Code	Elevation range m a.s.l.	#Sampled trees	Mean top height (std) cm	Mean shoot length (std) cm/year
Z. sicula	Ciranna bottom	ZS_CIR1	332–357	221 (221)	575.8[cd] (92.6)	9.4[d] (8.0)
	Ciranna slope	ZS_CIR2	318–355	31 (31)	294.8[de] (64.1)	7.8[d] (5.0)
	Pisano	ZS_PIS	495–526	67 (67)	362.8[de] (152.1)	7.6[d] (6.1)
	All			319 (319)	411.1[b] (135.7)	9.1[b] (8.0)
Z. abelicea	Levka Ori West	ZA_LEV_W	1070–1270	60 (60)	1244.2[a] (96.2)	27.4[a] (17.2)
	Levka Ori East	ZA_LEV_E	1156–1591	15 (65)	993.8[ab] (239.1)	15.4[c] (11.3)
	Kedros	ZA_KED	986–1280	8 (22)	660.2[c] (60.8)	21.4[b] (13.3)
	Psiloritis	ZA_PSI	1322–1335	13 (na)	546.8[cd] (163.9)	—
	Dikti South	ZA_DIK_S	1138–1644	5 (56)	798.1[bc] (129.8)	11.4[d] (6.9)
	Dikti North	ZA_DIK_N	1119–1247	23 (55)	674.0[c] (158.3)	11.7[d] (7.0)
	Thripti	ZA_THR	1145–1154	9 (75)	183.2[e] (252.0)	11.4[d] (7.3)
	All			133 (333)	728.6[a] (347.2)	16.6[a] (13.1)

Note: The number of sampled trees refers to top height or shoot length (in brackets). Significant differences at $p < 0.05$ are indicated with different letters for mean top heigth and mean shoot length; italics (in brackets) is std.
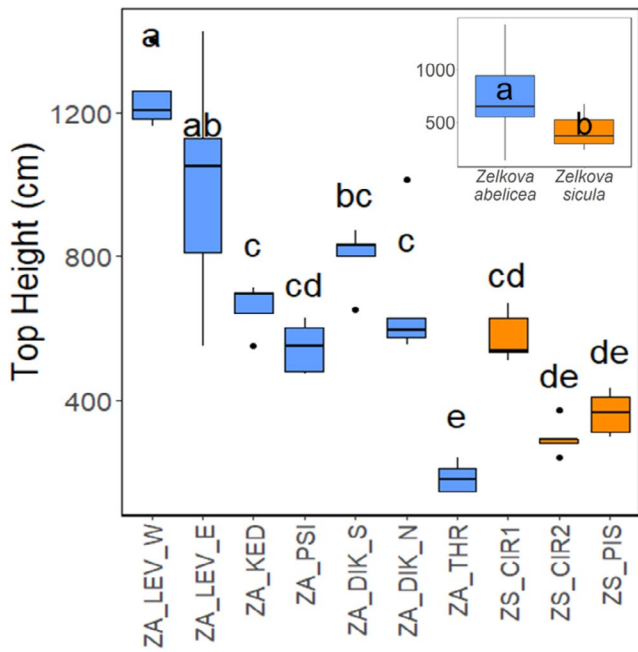
FIGURE 2 | Top height of the *Zelkova abelicea* and *Zelkova sicula* investigated stands. Populations are ordered according to a longitudinal gradient from west to east (*Z. abelicea*) or decreasing topographical suitability of the location (*Z. sicula*, cf. Garfì et al. 2021). The miniature shows boxplots for each species. Box size represents the interquartile range, the black line is the median, the whiskers indicate variability outside the upper and lower quartiles, and individual points are outliers. Different letters indicate significant differences at $p < 0.05$.

potential of this species. In most of the sampled wild trees, the growth rate was relatively faster across the first 10 years of life (up to 12–14 cm/year) but tended to sharply decrease (or even to become null) after that age, indicating that growth approximated (or reached) its maximum potential (Figure 3a,c). This trend was not the same for the cultivated tree, which continued to grow at a fast pace throughout the entire observation period (Figure 3b,d). At the same cambial age (28 years), the size of the cultivated tree was 7.5 times greater than that of the tallest wild tree, that is, 10.4 and 1.35 m, respectively, corresponding to average growth rates of 35.9 and 5.8 cm/year, respectively.

3.2 | Shoot Length

Similar to the TH, the difference in SL between the two *Zelkova* species was remarkable, as the mean value of the Cretan trees exceeded 1.8 times that of their Sicilian counterparts but could even reach threefold in the most favourable sites (Table 1). Furthermore, strong variability was observed within *Z. abelicea* at the stand level. A somewhat decreasing trend occurred from west to east (Figure 4), with the stands from Levka Ori and Kedros growing significantly more ($p < 0.01$) than those in eastern Crete. ZA_LEV_W again showed the best performance, with a mean value of 27.4 cm (± 17.2 cm) against 11.4 cm (± 7.3 cm) observed at ZA_THR. The SL of the three Sicilian stands was similar in magnitude to that of the *Z. abelicea* populations from the Dikti Mts. and Thripti Mts. The differences between these latter groups were not statistically significant ($p > 0.1$), irrespective of the species or population.

3.3 | Tree Ring-To-Climate Relationships

The tree ring attributes of the two species were compared, using for *Z. sicula* unpublished data and for *Z. abelicea* the data from a previous publication see Fazan et al. (2017 for details). The descriptive statistics for the raw tree-ring chronologies are shown in Table 2.

For *Z. sicula*, two trees were discarded after cross-dating because they were poorly synchronised with the rest of the tree ring series. The construction of individual chronologies by the method of 'serial sectioning of the trunk at equal intervals from the top to the base' (Kolishchuk 1990), in addition to overcoming any problem of missing rings, also made it possible to identify false tree rings/intra-annual density fluctuations. False rings were especially visible in the upper half of the stem length; they occurred in 1981, 1982, 1984–1986 and 1991 in four individuals and were synchronic for two of them. The series lengths ranged from 17 (1977–1993) to 68 (1926–1993) years, with an overall mean value of 35 years. The average raw ring width was 0.342 mm (minimum: 0.035 mm, maximum: 1.932 mm), that is, approximately a quarter of the width of its Cretan relative. The mean sensitivity (MSE) (0.432 for *Z. sicula* and 0.324 for *Z. abelicea*) and mean series intercorrelation (MSC) (0.609 for *Z. sicula* and 0.433 for *Z. abelicea*) were relatively high and greater for the Sicilian species. In contrast, autocorrelation (AC), that is, the statistical non independence of successive years of tree growth, was approximately 1.5 times greater for the Cretan species than for its Sicilian counterpart (0.621 vs. 0.448).

The response to climate showed fairly similar patterns between the two species but differed substantially by a one-month shift for the monthly climatic attributes most significantly correlated with growth (Figure 5). *Z. sicula* showed particularly sensitive (at least $p < 0.05$) to current April and May precipitation levels and negatively responsive to May temperatures (Table S6). Conversely, for *Z. abelicea*, the precipitation in May and June had a direct influence on growth, while the species reacted negatively to June temperatures. Furthermore, although not highly statistically significant ($p < 0.1$), some clues suggested that precipitation levels in February, March and September played a positive role in the growth of *Z. sicula*.

Similarly, a shift pattern was detected for the SPEI, which was positively correlated with growth ($p < 0.05$) in the period April–June (with isolated February) for *Z. sicula* and in the interval from May to August for *Z. abelicea*. Moreover, an additional weak positive correlation ($p < 0.1$) between the SPEI of July and September and tree growth was found for *Z. sicula*.

4 | Discussion

4.1 | Tree Size and Offset Drivers Among Refugia

The overall physiognomy of a forest mirrors how environmental factors affect the growth of trees. Optimal environments support luxuriant forests, whereas in sites where more or less severe abiotic constraints exist, trees grow poorly and productivity is low. Soil properties (fertility, drainage), climate (temperature and rainfall patterns), topography (altitude, aspect, convergent landforms) and biotic disturbances are largely known to be the
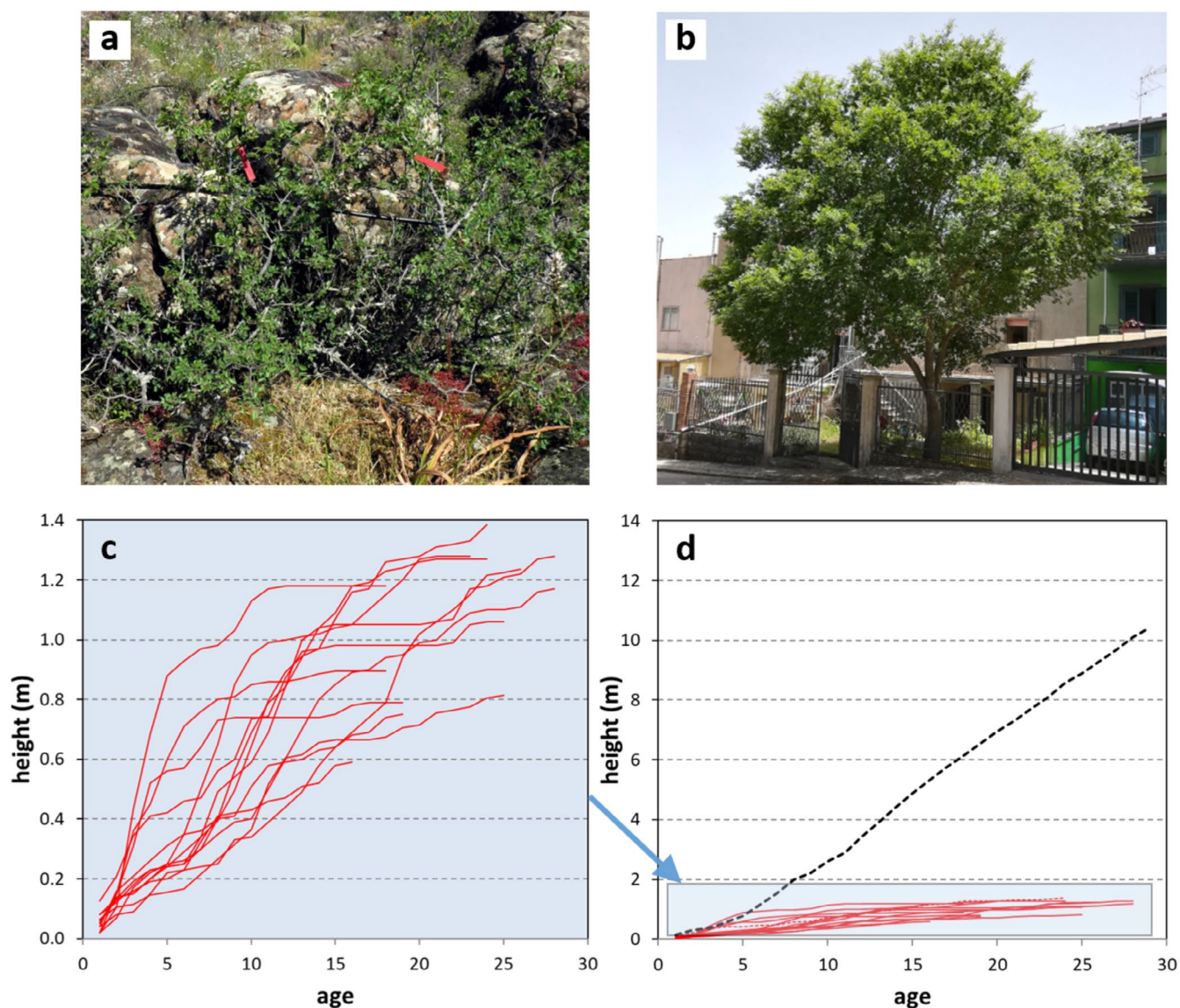
FIGURE 3 | Growth habit and height growth dynamics of *Zelkova sicula* individuals. (a) Typical dwarf shrub at Bosco Pisano. (b) Cultivated tree in a private garden. (c) Individual growth curves of wild trees constructed by stem analysis. (d) Growth curves of the cultivated tree drawn after annual measurement of shoot growth (black dotted line) and wild individuals (red solid lines) plotted at the same scale.

main drivers of tree growth (Vanclay 1992). According to the 'phytocentric method' (Skovsgaard and Vanclay 2008), many characteristics of vegetation have potential significance as ecologic indicators for assessing site quality. For a given species within a growth region, stand height might be the most practical productivity indicator. In particular, the potential maximum tree height or TH is most often considered a valuable metric for site productivity classification (Vanclay 1992; Zhou et al. 2019). Relict trees and their respective refugia do not deviate from the principles described above (Miller et al. 2010; Hampe and Jump 2011).

Although distinct inherent mechanisms related to specific genetic and/or physiological species traits could partly explain differences in growth performance (Oldeman 1990), in our case study several clues points to the possible differential functioning of the two sites. As suggested by the growth data and spatial patterns of the two *Zelkova* species, the variability in the site quality of the respective refugial areas could play a major role in the tree stand growth response. Overall, the environmental conditions of the Cretan refugia seem to be more suitable than those of their Sicilian counterparts for supporting the local climate relict. This appears demonstrated by both the TH and SL metrics, which are on average nearly two times greater for *Z. abelicea*, with individuals growing under more optimal conditions that can develop the growth form (*sensu* Hallé, Oldeman, and Tomlison 1978) of large trees up to 15 m tall. In contrast, even in the most favourable situations within its native range, *Z. sicula* cannot exceed the size of a shrub/small tree and has an annual SL growth rate that is three times smaller than that of the less water-limited populations of its Cretan relative.

However, a tree-like growth form is considered an exception in both species since, as a rule, the majority of the stands on either Sicily or Crete consist of scattered dwarf shrubs (Kozlowski et al. 2014). With this concern, distinct spatial patterns have already been highlighted for the Cretan relict populations versus the Sicilian counterparts. In the former, a west–east

decreasing tree size pattern has been associated with an eastward longitudinal gradient of rainfall reduction (Goedecke and Bergmeier 2018; Fazan et al. 2022); in the latter, the topographic positions of concave landforms against upper slopes likely represent the discriminant factor for increasingly poor growth (Garfì et al. 2011, 2021). In addition, as shown by the growth dynamics curves generated from the stem analysis of *Z. sicula*, we postulate for this species that, as a rule, after a phase of relatively rapid growth, the height increase in the native sites usually tends to decrease abruptly and culminates early (at approximately the age of 10 years in the studied tree sample). Accordingly, the observed small size, or in general the prevailing shrubby habit, can be assumed to be 'typical' for the species in the current habitat and is referred to as an adaptive strategy to environmental stress factors such as aridity. This feature has been shown to rely on internal structural traits such as narrow, short vessels (cf. Garfì,

Barbero, and Tessier 2002), which reduce the risk of embolism due to water stress during summer drought but increase resistance to sap flow, thus limiting height growth and finally resulting in the shrubby form (Baas and Schweingruber 1987; Cruiziat and Tyree 1990; Wilson 1995; Quero et al. 2011). This assumption seems corroborated by the evidence that, in contrast, the sole *Z. sicula* individual cultivated at a higher elevation, where drought stress is significantly mitigated, is the only known plant with a true tree habit (Figure 3b). Moreover, despite being more than 11 m tall at present, it is still growing at a notably higher rate (more than six times) than what has been observed in trees from the wild, and according to its growth-to-age curve shape, it has not yet achieved its maximum growth potential (Figure 3d).

All these clues point to the crucial role of surface water availability in the fitness of both Mediterranean relicts within their respective refugia. It is renowned that Cenozoic relict plants mainly prefer locations with wet climates and short dry seasons (Hampe and Jump 2011), and mountainous areas have often been reported as major refugia for this flora because they offer a wide array of sheltered habitats where conditions are usually milder and moister (Huang et al. 2015). As reported by Svenning (2003), the relict taxa that have persisted in the Mediterranean region throughout past climatic fluctuations generally belong to meso-macrothermic genera; however, they are relatively more drought-tolerant than extinct taxa. The processes underlying their persistence have been correlated with the existence of two types of refugia in the area: (i) cool, moist mid-altitude mountain refugia, which are relatively frequent, and (ii) warmer and probably more drought-prone refugia found in low-altitude valley-bottoms, occurring less commonly. These two scenarios match fairly well with the present-day distribution of Z. abelicea and Z. sicula, respectively. The Cretan relict is in fact restricted to the main mountain areas of the island, and studies on ecological niche modelling (Bosque et al. 2014; Goedecke and Bergmeier 2018) showed that elevation is one of the best predictors of its distribution. Alternatively, the isolated, low-altitude *Z. sicula* stands are exclusively sustained by hydrological microrefugia determined by terrain concavities (Garfì et al. 2021), where most likely the underground water supply can significantly compensate for insufficient surface water availability and can be pivotal for relative decoupling from the surrounding macroclimate (Dobrowski 2010; Lenoir, Hattab, and Pierre 2017). For both species, summer very likely represents the crucial period for their endurance, not only due to lower (or null) rainfall input in this season but also due to the occurrence of heatwaves, that is, consecutive days of unusually high temperatures (Hampe and Jump 2011; Barbeta and Peñuelas 2017). Such events may be responsible for a sharp increase in vapour pressure deficit, which can intensify the evapotranspiration rate and soil
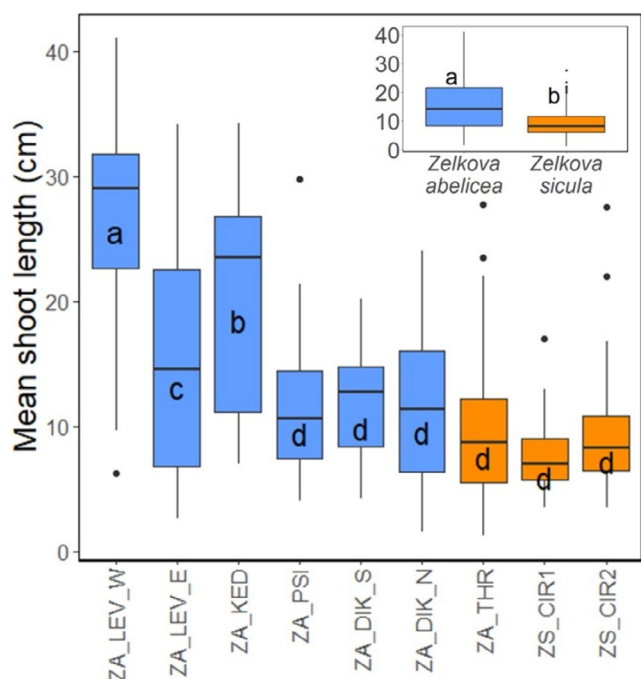
FIGURE 4 | Average maximum shoot length of the *Zelkova abelicea* and *Zelkova sicula* investigated stands. Populations are ordered according to a longitudinal gradient from west to east (*Z. abelicea*) or decreasing topographical suitability of the location (*Z. sicula*, cf. Garfì et al. 2021). The miniature shows boxplots for each species. Box size represents the interquartile range, the black line is the median, the whiskers indicate variability outside the upper and lower quartiles, and individual points are outliers. Different letters indicate significant differences at $p < 0.05$.

TABLE 2 | Descriptive statistics for the mean raw tree-ring chronologies of *Zelkova sicula* and *Zelkova abelicea*.

Species	# trees (elementary series)	Time span	MSL (min–max) (years)	MGR (mm/year)	MSE	MSC	AC
Zelkova sicula	14 (41)	1926–1993	35 (17–68)	0.34 ± 0.285	0.432	0.609	0.448
Zelkova abelicea[a]	74 (145)	1779–2012	92 (30–234)	1.32 ± 0.684	0.324	0.433	0.621

Abbreviations: AC, autocorrelation; MGR, mean growth rate; MSC, mean series intercorrelation; MSE, mean sensitivity; MSL, mean tree-ring series length.
[a]Data from Fazan et al. (2017).
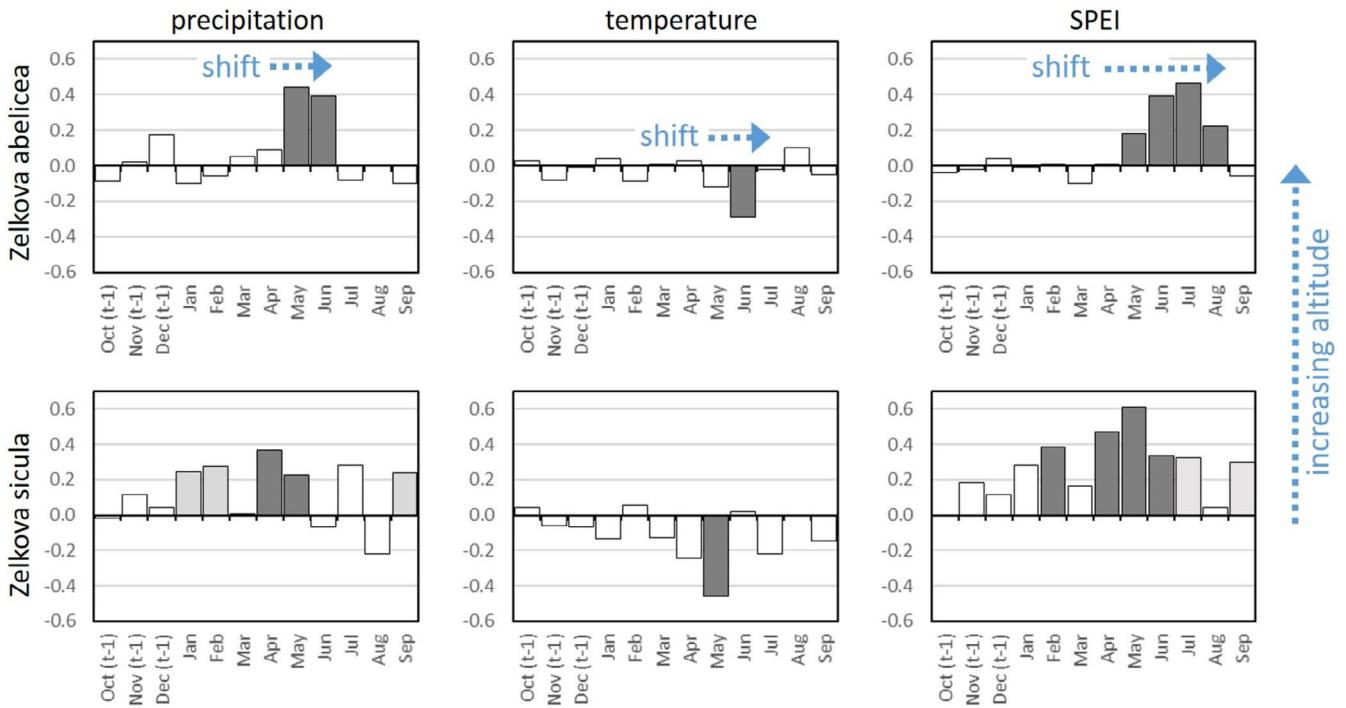
FIGURE 5 | Response functions from prior October to current September between the residual tree-ring chronology of *Zelkova abelicea* (top) and *Zelkova sicula* (bottom) and monthly precipitation sum (left), monthly maximum temperature (center) and 3-month SPEI (Standardised Precipitation-Evaporation Index) (right). Significant values are indicated in colour dark ($p < 0.05$) and light ($p < 0.1$). Data for *Z. abelicea* from Fazan et al. (2017).

water loss, resulting in greater water stress for plants (Ashcroft and Gollan 2013). As demonstrated in studies on the functioning of microrefugia in southeastern France hosting the southernmost marginal populations of wide-ranging species, heatwaves and vapour pressure deficit are remarkably alleviated at these special sites, which act as stable climatic enclaves decorrelated from the regional climate (Finocchiaro et al. 2024) wherein also typical climate relicts can persist over time.

However, among relicts, species or populations of species most often can experience ecological marginality even within microrefugia (Herrera and Bazaga 2008; Keppel et al. 2012; Woolbright et al. 2014), as plants may be able to endure macroclimatic limitations but do not flourish (Miller et al. 2010; Abeli et al. 2014). These aspects have been investigated in detail for *Z. sicula*, and it has been proven that the last remnants of this species currently grow at the extreme edge of its potential range (Garfì et al. 2021). Similarly, for *Z. abelicea*, the poor growth response of the easternmost stands (Fazan et al. 2022) points to a drift toward increasingly suboptimal environments from west to east, wherein the lower moisture supply with respect to the most suitable western refugia very likely plays a key role. Therefore, on the one side an 'elevation effect', entailing a significant attenuation of environmental constraints, seems to demonstrate the greater suitability of mountain refugia for the conservation of climate relicts and can be recognised as the major offsetting driver for the differential functioning mechanism of low- versus high-altitude refugia on the two Mediterranean islands. On the other side, as observed by the growth patterns of the Cretan relict throughout its entire distribution range, macroclimatic processes on a regional scale can involve additional diversification of this picture, locally blurring the effectiveness of refugia from a long-term conservation perspective.

4.2 | Radial Growth Differences Are Not Only a Matter of Heat and Humidity

The relationship between the tree-rings and climate of *Z. abelicea* was previously investigated by Fazan et al. (2017). However, in the present study, the interpretation of the results, carried out jointly with the dendroecological analysis of its close relative from Sicily, has provided new insights into the role and distinct functioning of refugia in the Mediterranean and their relationships with the sheltered relicts. Indeed, the two investigated tree species seems to effectively mirror the extreme ecological amplitude characterising their respective refugia. The Cretan sampled trees included large tree individuals all obtained from the most hydrologically favourable site for the species, namely, the Omalos polje in Levka Ori (W Crete), between 1125 and 1400 m a.s.l. Fazan et al. (2017). In contrast, for the Sicilian species, the sample selection only comprised tiny shrubs within the ZS_PIS population, which is situated at an elevation of approximately 500 m a.s.l.

As shown by all the descriptive statistics (Table 2) for the raw tree-ring chronologies, it was possible to extract a good climatic signal for both relicts. However, for this specific case study, it must be taken into account that causal external drivers other than climate, namely, the long history of anthropogenic disturbance, could have affected the radial growth of both the investigated stands. As largely documented for the whole island of Crete (Rackham and Moody 1996; Atherden and Hall 1999; Arvanitis 2011), intensive browsing in addition to evidence of pollarding and wildfire took place and is still (at least for browsing) ongoing throughout the mountainous areas of Crete, whereas diffuse grazing is an ancient customary practice in the Sicilian study area as well (Di Pasquale and Garfì 1989; Di

Pasquale, Garfì, and Migliozzi 2004). These processes might have noised, to some extent, the climatic signal of growth rings shared between trees and/or could also result in the formation of tiny and hardly datable or even missing rings.

At first glance, the comparison of the radial growth of the two species reiterates the same pattern as for the elongation growth, with *Z. abelicea* producing larger rings than its Sicilian relative. This evidence is clearly related to the different habit of the sampled plants, that is, trees on Crete vs. shrubs on Sicily, which as shown seems to mainly depend on the distinct suitability of the two sampling areas in sustaining their respective relict trees. Nevertheless, especially for *Z. sicula* the past impact of grazing on ring low growth rate, cannot be ignored, but as has been shown by the height growth dynamics (cf. the previous section) it seems to play no significant role in the typical shrubby habit of this species, which is assumed to depend mainly on climatic constraints.

In fact, as highlighted by the high MSC values, the individual ring series are well correlated with each other, reflecting good cross-dating and a common climatic signal in the investigated trees of each species, though more strongly for *Z. sicula* than for *Z. abelicea*. This difference can be related to the differential impact of anthropogenic disturbances on the sampled trees. For instance, not all *Z. abelicea* individuals could have been pollarded in the same year, resulting in perturbations that are not synchronously shared among all plants (Schweingruber 1988; Rackham and Moody 1996); conversely, the browsing pressure on *Z. sicula* can be assumed to affect all individuals more uniformly in space and time, resulting in a more homogenous growth response in this species. The MSE, which is a measure of the mean relative changes between adjacent ring widths, stays much > 0.15 for the two species, the threshold for considering a species to be complacent (Grissino-Mayer 2001). A value of 0.30 indicates a very high sensitivity of tree-ring growth to climate variability from year to year. Additionally, as expected, the MSE is greater for *Z. sicula*, highlighting that the environment of the Sicilian relict is harsher and prone to stronger climatic fluctuations and aridity (Fritts 1976; Touchan et al. 2016) than that of its Cretan counterpart. This assumption is also supported by the opposite pattern of the AC data (0.448 and 0.621 for *Z. sicula* and *Z. abelicea*, respectively), which is reflective of the poorly delayed effect of the previous year's growth on the current year's ring width within *Z. sicula*; it highlights the prominent role of unpredictable annual climate fluctuations on its growth, and the negligibility of other external factors. Interestingly, in addition to its Cretan relative, the AC values are also noticeably lower than those of other deciduous or semideciduous broadleaved trees investigated in Sicily and other circum-Mediterranean areas, such as *Celtis australis* L. (Garfì 2000), *Quercus pubescens* (Serre-Bachet 1982; Martinelli, Pignatelli, and Romagnoli 1994; Garfì 2000), *Q. cerris* L. (Martinelli, Pignatelli, and Romagnoli 1994), *Q. robur* L. (Nola 1991; Rozas 2005) and *Q. gussonei* (Borzì) Brullo (Sala 2016). Unlike *Z. abelicea* and the above-cited broadleaved species, the impact of grazing on *Z. sicula* can be invoked as a prominent factor to explain this divergence. Such permanent pressure, which leads to the regular suppression of vegetative shoots and leaf biomass, can be evoked as the responsible for a sharp reduction in photosynthetic effectiveness and in the production rate of assimilates, which are essential for radial growth (McLaren and Peterson 1994). During each vegetative

cycle, fewer reserves are stored in the parenchymal tissues of plants, and in the following growing season these limited resources are therefore entirely mobilised for leaf expansion and new crown formation (Schweingruber 1988). Accordingly, since the resource supplies remain negligible (or even null), tree-ring growth patterns are almost entirely dependent on variations in the climatic factors of the current year.

In light of the above, despite the influence of biotic factors that may create noise in ring growth magnitude, the main dendrochronological descriptors show that climate still remains the major driver of tree growth, acting differently on the two relict species depending on the locally distinct geographic and microtopographic features of the two refugial areas.

4.3 | Elevation-Related Impact of Climate on Tree-Ring Growth Patterns

The 1-month shift in the profile of response functions is the main distinctive feature of the tree ring–climate relationships between the two species and offers further insight into the diverse compensatory drivers between the two insular refugia.

In a majority of studies on tree ring response to climate in the Mediterranean area, the role of precipitation has proven to be crucial for tree growth (e.g., Touchan et al. 2014, 2017). This was also demonstrated in investigations carried out on tree species growing in the close vicinity of the two Mediterranean *Zelkova* species, such as *Celtis australis* and *Quercus pubescens* in Sicily (Garfì 2000) and, albeit to a lesser extent, *Cupressus sempervirens* L. in Crete (Fazan 2014). In the present case study, the strongest climatic signal is confined to late-spring and early-summer precipitation, namely, April–May for the Sicilian relict and May–June for its Cretan counterpart, with weak or no correlation with previous autumn-winter precipitation, as commonly observed in different species from the Eastern Mediterranean (Touchan et al. 2014). Interestingly, also the growing season temperature, which negatively impacts the ring width of both *Zelkova* species, is delayed by 1 month, that is, from May in Sicily to June in Crete. The combination of the positive correlation of precipitation and the negative response to temperature throughout the growing season suggests that radial growth is definitively controlled by evapotranspiration processes and water balance. This assumption is corroborated by the positive relationship between tree growth and the SPEI, which reflects the high sensitivity of both species to drought conditions occurring during the growing period. Moreover, for the individual monthly attributes, the impact of evapotranspiration starts earlier for the low-elevation Sicilian trees and ends later for the higher-elevation Cretan stands. Overall, the integrated effects of precipitation and evapotranspiration throughout the vegetative period have been detected in other deciduous and evergreen broadleaved trees of the Mediterranean area, such as *Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Q. ilex*, and *Q. pubescens* (Campelo et al. 2009; Cherubini et al. 2003; Di Filippo et al. 2010; Nijland et al. 2011; Lebourgeois et al. 2012). As reported in earlier research (Bréda and Granier 1996; González and Eckstein 2003), in several ring-porous trees, such as *Zelkova* spp., the formation of earlywood tissues usually occurs before the onset of leaves. This suggests that in both of the investigated *Zelkova* species the water

balance in late spring-early summer is of major importance for growth because most of the latewood, which largely contributes to the total yearly ring width, is formed at that time (Di Filippo et al. 2010). Later, as the hot and dry season progresses, the significant increase in the evapotranspiration rate likely induces the cessation of any growth processes and, as repeatedly recorded for *Z. sicula* (Garfì, Barbero, and Tessier 2002), may even trigger tree decline and dieback in the event of severe drought.

However, the shift of all the most significant climatic attributes in the response of the two relict trees seems to reflect the distinct role of their refugia on growth performance and adaptation to the current habitat variability. As highlighted by investigations based on a network of 79 tree-ring chronologies from different species and a range of elevations in the eastern Mediterranean (Touchan et al. 2014, 2016), the tree growth response tends to be stratified by elevation since high mountain climate regimes determined by variable topography and/or orography can involve similar signals in chronologies at comparable altitudes even from widely separate locations. Accordingly, the relatively low temperatures in the Cretan mountains most probably induce longer bud dormancy in *Z. abelicea*, delaying the onset of growth resumption (Touchan et al. 2017). In contrast, at the low-elevation site of *Z. sicula*, the growth processes very likely resume earlier according to an earlier rise in spring temperatures. On the other hand, plant growth is susceptible to cease as the effects of evapotranspiration and water loss increase beyond the threshold of tolerance for plants and/or the capacity of the microrefugium to buffer against the regional macroclimate (Finocchiaro et al. 2024). These distinct phenological patterns also point toward additional species-specific growth peculiarities of the Sicilian relict, as also suggested by the positive (although weak) correlation of growth with the late winter precipitation that occurs shortly before growth resumption. Moreover, this signal is often recorded in central-western Mediterranean tree chronologies (Touchan et al. 2017), whereas it is usually absent in species from the eastern portion of the Mediterranean Basin (Touchan et al. 2014), as is also the case for *Z. abelicea* Fazan et al. (2017). Such evidence can be explained by the crucial role of groundwater stored in the soil during the rainy season, which can support plant growth by alleviating water stress when surface soil moisture is depleted (Le Roux et al. 2013; McLaughlin et al. 2017). A review concerning a wide range of species (Barbeta and Peñuelas 2017) showed that groundwater uptake is more likely to occur in water-limited ecosystems, and this probability significantly increases in the dry season. However, soil moisture may vary with depth due to an array of factors influencing vertical drainage, such as texture, diffuse rockiness or hydrophobic layers. Therefore, shallower soils can dry out under direct sunlight conditions even if the vapour pressure deficit is low, while moisture remains longer in deeper soils and in the presence of a high clay content, which improves the water holding capacity (Ashcroft and Gollan 2013; McLaughlin et al. 2017; Garfì et al. 2021). At the ZS_PIS site, the local soils are very clayey (52% clay, 32% loam, 16% sand, unpublished) and rich in rock outcrops, unlike at Omalos polje, where the investigated *Z. abelicea* trees mainly grow on steep slopes with thin sandy-loam to silty-loam soils (Fazan et al. 2022). These features likely result in greater permeability and lower water holding capacity of soils, therefore accounting for the lack of groundwater-related signal in the response of the Cretan relict trees to winter precipitation.

Conversely, groundwater uptake has been assumed to be crucial for the functioning of the hydrological microrefugium hosting the current populations of *Z. sicula* and is most likely the key driver supporting the species endurance in its current habitat, as reported in Garfì et al. 2021. Another behavioural trait seems to be exclusive to the Sicilian relict, mirroring either its adaptive ability to the harsher environment or, in turn, the distinctive functioning of its low-elevation refuge. The positive, albeit weak, correlation between ring growth and precipitation in September is a clue to the possible resumption of vegetative activity in late summer. This pattern is confirmed by the presence of false rings in some of the sampled trees, coupled with the emission of a second elongation shoot often observed in that season (Garfì, personal observation). Such events most likely rely on anticipated and unusually abundant autumn rainfall associated with less extreme temperatures, which are still well above the threshold for metabolic functions to occur (Edmondson 2010) before the definitive winter dormancy. In the event of such favourable conditions, this type of reaction may be additionally interpreted as a reiterative response of plants to crown withering/desiccation injuries triggered by severe water stress in summer (Hallé, Oldeman, and Tomlison 1978; Garfì, Barbero, and Tessier 2002). These sequential shoot flushes interrupted by a resting phase during a dry season within the same vegetative period are defined as polycyclic growth. This is a common feature in trees typical of moist tropical climates and may represent an adaptive process of drought avoidance, which is also observed in some Mediterranean woody species (Hover et al. 2017; Tondjo et al. 2018). In the years concerned, the release of a second sprout may induce the production of an unusually larger growth ring.

5 | Conclusions

The growth performance and adaptive ability of the two investigated relict species provide integrated insight into the diverse functions and processes of Mediterranean refugia. In this case study their distinct suitability in sustaining the respective climate relicts basically appears to depend on the differential role of elevation versus micro-topographical features in decoupling from the regional climate, revealing that the high elevation refugia seem more effective in the long term conservation perspective. Although their effectiveness relies on apparently distinct mechanisms, both habitat characteristics seems ultimately related to water balance and evapotranspiration processes, which are probably the key drivers in maintaining these two mesophilous relict species.

We can speculate that the evolutionary history of the two insular *Zelkova* relicts initially followed similar or possibly common patterns, leading both species to escape the constraints of Pleistocene glacial events colonising suitable refugia at lower latitudes and elevation. Nevertheless, after post-glacial warming, their fates began to diverge. *Z. abelicea* was able to regain more suitable environments by migrating to higher altitudes where it was possible to compensate for the thermal extremes and moisture deficit. In contrast, *Z. sicula* could have faced a more complex history. It is possible that triploid and sterile populations (cf. Garfì et al. 2021) coexisted for some time with their diploid and fertile relatives. On the one hand, it can be assumed that during interglacial phases or after post-glacial warming, fertile

individuals could have migrated to a higher elevation, up to the top of the Hyblean massif (almost 1000 m a.s.l.). From these locations, they would have subsequently disappeared in historical times, along with almost the entire forest cover, mainly due to anthropogenic causes, whereas only some triploid individuals/populations were able to accidentally persist at very few sites. On the other hand, it is also likely that no fertile individuals were able to disperse across the climatic barriers that characterise the harsher lower plains, separating them from the high mountain ranges of northern Sicily, which today probably would offer more suitable habitats for this mesophilous species. Therefore, *Z. sicula* remained imprisoned within the current low-altitude enclaves (Garfì et al. 2021) of the Sicilian inland areas where, most likely due to the particularly favourable moisture conditions provided by localised hydrological microrefugia, it was allowed to survive but in conditions of extreme marginality.

Author Contributions

Acknowledgements

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All raw data used for the manuscript preparation are available in the Supporting Information, Tables S2–S6.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.