Department of Biology
University of Fribourg (Switzerland)

Thousands of years of solitude: past, present and future of relict trees in the Mediterranean – the case of *Zelkova abelicea* from Crete

THESIS

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Laurence Fazan

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Laurence Fazan https://orcid.org/0000-0002-2981-1806

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Thesis supervisor

Prof. tit. Gregor Kozlowski

Dean

Prof. Ulrich Ultes-Nitsche

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SUMMARY

Zelkova abelicea (Lam.) Boiss. (Ulmaceae) is a tree species endemic to the mountains of the Mediterranean island of Crete (Greece). This species is classified as endangered (EN) on the IUCN Red List of threatened species. Unsustainable pastoral practices are the main threat for the species. Most *Z. abelicea* populations are heavily browsed by goats, which strongly limit the growth of young or small individuals, hinder the production of fruit and the survival of seedlings, and keep individuals in a dwarfed stunted state, oftentimes during decades or centuries. Some *Z. abelicea* populations are composed uniquely of dwarfed individuals. Trampling by both goats or sheep as well as dry summer conditions also prevents seedlings from establishing and surviving. *Zelkova abelicea* has been the subject of only a handful of studies up to present, despite being one of the most emblematic trees of Crete and having a strong local patrimonial value. It is one of the few tree species to thrive throughout the mountains of Crete and therefore has an important ecosystemic value. Increasing the scientific knowledge of a species is not only important in order to better understand the species and establish a state of the situation at a given time, but is also important to better carry out and pinpoint applied conservation actions in the scope of a long-term preservation of the species. In this thesis, I have tried to address several knowledge gaps concerning *Z. abelicea*.

In **Chapter 1**, I explore the changes in growth and reaction through time of *Z. abelicea* individuals found within permanent fenced plots in which no browsing occurs. I compare the growth of these non-browsed *Z. abelicea* individuals with the growth of overbrowsed individuals found in unfenced areas. My results reveal the high impact of the current (over)browsing pressure on shoot elongation and height increase of the species. Indeed, protected from browsing *Z. abelicea* individuals grow on average twice as much as their non-protected counterparts in the same given time. I also show that growth in protected areas is maximal in the first two years after fencing and gradually decreases afterwards, and that taller individuals tend to grow more than shorter ones. My research shows that protection against browsing over several consecutive years is sufficient to allow prostrate, dwarfed *Z. abelicea* individuals to reach a height sufficient to escape browsing by goats.

In **Chapter 2**, I go further in investigating *Z. abelicea* growth patterns in fenced plots. Here, I compare growth between protected sites that are located throughout the distribution range of the species from western Crete (Levka Ori Mountains), central Crete (Mt. Kedros) and eastern Crete (Dikti Mountains and Thripti Mountains). I show that the growth of non-browsed *Z. abelicea* individuals is different according to locality. More specifically, I found a longitudinal gradient in growth, as trees from fenced plots in western and central Crete grow twice as much in the same given time than those situated in eastern Crete. I investigated a wide dataset of climatic, edaphic, physiognomic and geographical variables to try to

understand these growth differences. I found that soil characteristics do not seem to influence *Z. abelicea* growth but that precipitation patterns in specific months seem crucial in determining *Z. abelicea* growth, and that growth in non-browsed Z. *abelicea* individuals seems to be reflective of a west to east decreasing precipitation gradient throughout Crete. I show that *Z. abelicea* individuals from the easternmost population of Thripti not only grow less but are also smaller than individuals of the other investigated sites, highlighting the extreme marginality of this easternmost *Z. abelicea* outpost.

In **Chapter 3**, I study dispersal unit traits of *Z. abelicea* and their variability as well as several traits related to fruit weight and fruit soundness (i.e. proportion of fruits with non-sterile seeds) across the distribution range of the species. *Zelkova* species have particular dispersal unit structures that are unique amongst Angiosperms. In autumn, whole shoots with leaves and fruits abscise from the trees and disperse mainly through anemochory (wind) or barochory (gravity). In addition, *Z. abelicea* trees produce fruits in masting events every two to three years. In this chapter, I study for the first time the characteristics of dispersal unit and fruit traits for *Z. abelicea* throughout the distribution range of the species. I show that most traits show a high variability among individual trees and less variability between mountain ranges. In addition, I provide the first measurements and analyses of fruit weight and seed sterility over the whole distribution range of *Z. abelicea.* I confirm that seed sterility in *Z. abelicea* trees follows a longitudinal gradient similar to the one found in the previous chapters for tree growth. Trees outside of the westernmost mountain range of Crete mostly have extremely high values of seed sterility, and a majority of investigated trees were found to be devoid of fertile seeds. These results help explain why regeneration through seedlings has almost never been observed in recent years outside of the westernmost mountain range for *Z. abelicea*. My study also showed that trees with high rates of seed sterility oftentimes are smaller and have shorter dispersal units with less leaves and fruits. Furthermore, my investigations allowed me to put into light the effects on fruit production of a gall midge species (Cecidomyiidae) affecting flowers of *Z. abelicea* and showed that this species has no significant impact on the production of fertile seeds but impacts the produced quantity and weight of fruits.

In **Chapter 4**, I concentrate on studying the biodiversity of epiphytic lichens and bryophytes associated with *Z. abelicea* trees in overbrowsed areas. This topic had previously never been addressed for *Z. abelicea*. My results show that *Z. abelicea* hosts a high number of epiphytic species. *Zelkova abelicea* trees from the westernmost mountain range (Levka Ori) have the highest lichen diversity, while trees situated on Mt. Kedros in central Crete have the highest diversity of bryophytes. Geographic position, browsing intensity and tree morphology (dwarfed or arborescent) are important factors in influencing the type of epiphytic community found on *Z. abelicea* trees. Interestingly, dwarfed individuals were found to have as much epiphytic diversity as arborescent trees. I show that high epiphytic diversity is found in some sites despite signs of strong disturbance due to pastoral activities and suggest the co-occurrence of disturbance tolerant and sensitive epiphytic species. The finding of several species previously unknown to Crete or even Greece showed how much is still to be discovered in the area.

The findings highlighted in this thesis are coherent and complementary. Indeed, I showed the strong impact of pastoral activities, namely browsing pressure, on *Z. abelicea* growth in unprotected areas. Despite the intensity of this disturbance, a high epiphytic diversity was found throughout most investigated places on Crete, and not only for arborescent trees but also for dwarfed individuals that are under the (almost) constant stress of goat appetite. The results of this thesis point towards the strong influence of climatic factors, and more precisely precipitation patterns, in influencing *Z. abelicea* growth and sexual reproduction. Trees, populations and epiphytes of *Z. abelicea* in the Levka Ori and on Mt. Kedros seem to perform better than those of Mt. Psiloritis, of the Dikti Mountains and of the Thripti Mountains. The easternmost *Z. abelicea* populations seem to be under stress due to the current climatic conditions and this trend will probably intensify within the next decades. This raises a strong and unsettling concern for the long-term survival and regeneration of the easternmost *Z. abelicea* populations, let alone along the whole range of the species. However, *Z. abelicea* may continue to astonish us with regards to its resilience capacities and adaptability. After all, the species has maintained itself and possibly spread vegetatively under strong browsing pressure and changing conditions during millennia in areas where no other tree species could establish or propagate in the Cretan mountains.

RÉSUMÉ

Zelkova abelicea (Lam.) Boiss. (Ulmaceae) est une espèce d’arbre endémique aux montagnes de l’île méditerranéenne de Crète (Grèce). Cette espèce est classée comme étant en danger d’extinction (EN) sur la liste rouge des espèces menacées de l’UICN. La menace principale pour l’espèce provient des pratiques pastorales non-durables. La majorité des populations de *Z. abelicea* sont intensément broutées par les chèvres, ce qui limite fortement la croissance des individus jeunes ou de petite taille, empêche la production de fruits, diminue la survie des plantules et maintient les individus sous une forme naine et rabougrie, souvent pendant des décennies ou siècles. Ainsi, certaines populations de *Z. abelicea* sont composées uniquement d’individus nains. Le piétinement par les troupeaux de moutons et de chèvres ainsi que les conditions de sécheresse estivale empêchent les plantules de s’établir et de survivre. *Zelkova abelicea* a fait l’objet seulement d’une poignée d’études jusqu’à présent, malgré le fait que cet arbre possède une forte valeur patrimoniale et soit parmi les espèces les plus emblématiques de Crète. C’est aussi une des seules espèces d’arbres à croitre à travers tous les massifs montagneux de Crète, ce qui lui confère aussi une importante valeur écosystémique. L’amélioration des connaissances scientifiques sur *Z. abelicea* n’est pas seulement importante afin de mieux comprendre l’espèce et établir un état de la situation à un moment donné, mais également afin de mieux cibler et mener des actions appliquées de conservation dans le cadre d’une préservation à long terme de l’espèce. Dans cette thèse, j’ai essayé de combler plusieurs lacunes de connaissances sur *Z. abelicea*.

Dans le **premier chapitre**, j’explore les changements de croissance et la réaction dans le temps d’individus de *Z. abelicea* qui ne sont plus broutés car situés dans des parcelles clôturées. Je compare la croissance de ces individus avec la croissance d’individus surpâturés situés dans des zones non-protégées. Mon étude met en lumière le fort impact du (sur)pâturage actuel sur l’élongation des pousses et la croissance apicale de *Z. abelicea*. En effet, les individus de *Z. abelicea* qui sont protégés du broutage grandissent en moyenne deux fois plus en taille, dans le même laps de temps, que leurs homologues broutés. J’ai également pu mettre en avant le fait que la croissance est maximale la première ou deuxième année après la pose des clôtures et diminue graduellement les années suivantes. De plus, j’ai observé que les individus initialement de grande taille ont tendance à pousser proportionnellement plus rapidement que les individus de taille plus modeste. Mon étude suggère qu’une protection contre le broutage, mise en place durant plusieurs années consécutives, est suffisante pour permettre aux buissons nains de *Z. abelicea* d’atteindre une taille suffisante pour échapper à la pression de broutage exercée par les chèvres.

Dans le **deuxième chapitre**, j’investigue de manière plus approfondie les schémas de croissance de *Z. abelicea* dans les parcelles clôturées. Ici je compare la croissance d’individus

dans des sites protégés du surpâturage à travers l'aire de distribution de l'espèce, à l'ouest (Levka Ori), au centre (Mt. Kedros) et à l'est (Mts. Dikti et Thripti) de la Crète. J'ai découvert que la croissance d'individus de *Z. abelicea* protégés du broutage suivait un gradient longitudinal à travers l'île. En effet, les arbres poussant dans les montagnes de l'ouest ou du centre de l'île poussent deux fois plus durant le même laps de temps que les individus situés à l'est de la Crète. J'ai étudié un large panel de variables climatiques, édaphiques, physiologiques et géographiques pour essayer de comprendre la cause qui explique ces différences de croissance. J'ai trouvé que les caractéristiques édaphiques des différents sites n'exercent aucune influence sur la croissance de *Z. abelicea* mais que le régime de précipitation durant certains mois est crucial. En effet, la croissance d'individus non broutés de *Z. abelicea* est corrélée au gradient de précipitations qui diminue d'ouest en est en Crète. J'ai découvert que les individus de *Z. abelicea* de la population (Thripti) la plus à l'est de l'île produisaient des pousses moins longues qu'ailleurs, mais également qu'ils étaient plus petits. Ceci souligne l'extrême marginalité de la population la plus orientale de Z. *abelicea*.

Dans le **troisième chapitre**, j'étudie la structure des rameaux de dispersion de *Z. abelicea* et la variabilité de leurs traits ainsi que plusieurs traits en lien avec la stérilité des graines et le poids des fruits à travers l'aire de répartition de l'espèce. Les espèces du genre *Zelkova* ont des rameaux de dispersion ayant une structure unique parmi les Angiospermes. En automne, des rameaux entiers avec feuilles et fruits se détachent des arbres et se dispersent par anémochorie (vent) ou barochorie (gravité). De plus, tous les deux à trois ans, les arbres de *Z. abelicea* fleurissent et produisent en masse et de manière synchrone leurs fruits (phénomènes de « mast »). Dans ce chapitre, j'étudie pour la première fois les caractéristiques des rameaux de dispersion et des fruits à travers toute l'aire de répartition de *Z. abelicea*. Mon étude suggère que la plupart des traits des rameaux de dispersion ont une forte variabilité interindividuelle, et qu'ils montrent moins de variabilité entre les différents massifs montagneux. De plus, je mesure et analyse pour la première fois à travers toute l'aire de répartition de l'espèce le poids des fruits et le pourcentage de stérilité des graines. J'ai pu confirmer que la stérilité des graines chez *Z. abelicea* suit un gradient longitudinal et reflète celui trouvé dans les précédents chapitres pour la croissance des arbres. Les individus de *Z. abelicea* situés en dehors du massif montagneux le plus à l'ouest de l'île ont pour la plupart des valeurs extrêmement élevées de stérilité des graines, et une grande majorité de ces arbres n'avaient aucune graine fertile. Ces résultats permettent d'expliquer pourquoi les plantules de *Z. abelicea* sont rarement observées en dehors de l'ouest de la Crète. Mon étude suggère aussi que ces arbres sont souvent plus petits et ont des rameaux de dispersion plus petits, avec moins de feuilles et de fruits. Par ailleurs, mes investigations ont pu mettre en lumière l'existence et l'impact sur la production de fruits d'une cécidomyie (Insecta, Cecidomyiidae) qui provoque des galles sur les fleurs de *Z. abelicea*. J'ai pu montrer que malgré la présence parfois très abondante de galles, l'insecte n'influence pas le taux de stérilité des graines, mais influence la quantité de fruits produits ainsi que leur poids.

Dans le **quatrième chapitre**, j'étudie la biodiversité des lichens et bryophytes épiphytes de *Z. abelicea* dans des zones surpâturées. Ce sujet n'avait jamais été étudié auparavant. Mes résultats suggèrent que la diversité d'épiphytes poussant sur *Z. abelicea* est relativement élevée. Les individus de *Z. abelicea* présents dans la montagne la plus occidentale (Levka Ori) de l'île possèdent la plus haute diversité de lichens, tandis que les individus présents sur le Mt. Kedros au centre de l'île ont la plus haute diversité de bryophytes. Les facteurs qui influencent le plus le type de communauté d'épiphytes de Z*. abelicea* sont la position géographique, l'intensité du broutage et la morphologie de l'individu (nain ou arbre). Je montre que les individus nains possèdent une diversité d'épiphytes aussi élevée que les individus arborescents. Mon étude révèle qu'une forte diversité d'épiphytes peut coïncider avec une forte pression pastorale et que cela suggère la cooccurrence d'espèces d'épiphytes sensibles et d'espèces tolérantes à la perturbation. Le fait que j'ai trouvé plusieurs espèces d'épiphytes précédemment inconnues de Crète ou même de Grèce montre un grand potentiel de recherche et de découvertes dans la région.

Pour conclure, les résultats mis en avant dans cette thèse sont complémentaires et cohérents les uns avec les autres. En effet, j'ai souligné la forte pression du broutage sur la croissance des individus de *Z. abelicea* dans les zones non protégées. Malgré cette pression, une riche diversité d'espèces épiphytes a été trouvée à travers plusieurs régions de Crète. Ceci a été révélé non seulement sur des individus arborescents poussant hors d'atteinte des chèvres, mais également sur des individus nains sous emprise (quasi) constante de l'appétit des chèvres. De plus, tous mes résultats tendent à montrer la forte influence des conditions climatiques, et plus particulièrement des régimes de précipitation, sur la croissance et la reproduction sexuée de *Z. abelicea*. Les individus, populations et épiphytes de *Z. abelicea* situés dans les Levka Ori et sur le Mt. Kedros semblent mieux se porter que ceux des Mts. Psiloritis, Dikti et Thripti. Les populations de *Z. abelicea* les plus orientales semblent être sous stress dû aux conditions climatiques actuelles et cette tendance va probablement s'intensifier durant les prochaines décennies. Cette observation soulève des questions quant à la survie et la régénération sur le long-terme des populations les plus orientales de *Z. abelicea* et dans une plus large mesure de toute l'aire de répartition de l'espèce. Cependant, *Z. abelicea* n'a pas fini de nous étonner en ce qui concerne ses capacités de résilience et d'adaptation. Au final, l'espèce s'est maintenue et s'est possiblement aussi propagée de manière végétative durant des millénaires dans les montagnes de Crète dans des endroits où aucune autre espèce d'arbre n'a pu s'établir ou se maintenir, malgré une forte pression pastorale et des conditions environnementales changeantes.

GENERAL INTRODUCTION

On the island of Crete (Greece), browsing has a very long history, and appeared before the introduction of domesticated animals. Indeed, a diverse community of wild browsers (several deer species, a dwarf elephant and a dwarf hippopotamus species) existed on the island long before the arrival of domesticated goats (Papanastasis 1998, Rackham and Moody 1996, Van der Geer et al. 2006). A lot of endemic plants on Crete therefore show specific adaptations or have developed avoidance strategies towards this long-lasting browsing pressure and have thrived in this way for centuries (Papanastasis 1998, Rackham and Moody 1996). Small-scaled, extensive and sustainable pastoralism has been carried out for centuries or even millennia on Crete, shaping the landscape and ecosystems (Hill et al. 1998, Ispikoudis et al. 1999, Kosmas et al. 2015, 2016, Lorent et al. 2009). However, following the socioeconomic transformations that occurred during the second half of the 20th century, herding underwent drastic changes on Crete, as in other places in Greece (Hadjigeorgiou 2011, Ispikoudis et al. 1993). Although pastoral activities were abandoned in many areas, the Cretan mountains saw an increase in the number of sheep and goats, oftentimes surpassing the carrying capacity of the local rangelands (Ispikoudis et al. 1993, Kosmas et al. 2015, Lyrintzis 1996). Flocks are less numerous but larger than before, and less mobile due to the almost complete abandonment of traditional transhumance patterns (Hadjigeorgiou 2011, Kizos et al. 2014, Kosmas et al. 2015). Some remote mountainous areas have become more accessible due to the creation of mountain roads (Hill et al. 1998, Hostert et al. 2003), and flocks often rely on external feed in addition to local vegetation (Hadjigeorgiou 2011, Kosmas et al. 2015).

The lack of sustainable management of these flocks has put an important pressure on the local vegetation in specific areas (Kairis et al. 2015, Papanastasis 1998). This is the case for the areas in which *Zelkova abelicea* (Lam.) Boiss. (Ulmaceae) grows. The genus *Zelkova* is a widespread Paleogene relict which nowadays has a disjunct distribution (Kozlowski and Gratzfeld 2013). Three species occur in eastern Asia: *Z. serrata* (Thun.) Makino, *Z. schneideriana* Hand.-Mazz., and *Z. sinica* C.K. Schneid. One species occurs in the Transcaucasian region: *Z. carpinifolia* (Pall.) K. Koch. The two remaining species are found in completely different climates and are endemic and restricted to two Mediterranean islands: *Z. sicula* Di Pasq. Garfì & Quézel on Sicily and *Z. abelicea* on Crete (Kozlowski et al. 2018, Garfì et al. 2021). On Crete, populations of *Z. abelicea* are found growing solely in the five main mountainous regions of the island and above 900 m a.s.l. (Egli 1997, Kozlowski et al. 2014, Søndergaard & Egli 2006). The species has the particularity of being able to propagate vegetatively through root suckering and to survive for centuries in a stunted dwarfed form with very slow growth due to overbrowsing (Egli 1997, Fazan et al. 2012, Søndergaard & Egli

2006). Individuals that are not browsed or that have escaped browsing will eventually develop into arborescent, 15-20 m trees, which are estimated to compose only ca. 5% of all known *Z. abelicea* individuals (Fazan et al. 2012, Kozlowski et al. 2014). A high intra- and interpopulation genetic diversity was found for *Z. abelicea*. The species also showed a strong genetic structuring and isolation by distance between mountains (Christe et al. 2014).

From 2014 to 2021, a project for the conservation of *Z. abelicea* was carried out on Crete (Abelitsia 2022, Zelkova 2022). One action of the project was to install permanent fenced plots throughout the distribution range of the species in order to completely exclude browsing and allow the growth of overbrowsed *Z. abelicea* stands, while monitoring every year the growth of the fenced individuals. I used the data from these monitoring activities to compare the growth of *Z. abelicea* individuals in overbrowsed versus protected areas, to study how *Z. abelicea* grew over several consecutive years in the absence of browsing pressure, and to see if any temporal or spatial differences could be seen. Another action of the project led to the collection of *Z. abelicea* seeds for propagation activities. Thousands of seeds were collected but only small amounts germinated and grew into seedlings. These findings led me to investigate seed sterility in *Z. abelicea* and its dispersal units. During the conservation project, our research team noticed that only few studies had been made regarding the species associated with or that grew on *Z. abelicea* (e.g. see Bauer and Bergmeier 2011, Gwiazdowicz et al. 2022, Hilszczanski 2011, Spribille et al. 2006, Stathakis 2011). In the last chapter of this thesis, I have therefore added to the topic by studying the epiphytic lichen and bryophyte communities associated with *Z. abelicea*.

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CHAPTER 1

FREE BEHIND BARS: EFFECTS OF BROWSING EXCLUSION ON THE GROWTH AND REGENERATION OF *ZELKOVA ABELICEA*

Laurence Fazan, Dany Ghosn, Ilektra Remoundou, Panagiota Gotsiou, Costas Thanos, Salvatore Pasta, Giuseppe Garfì, Gregor Kozlowski

Author contributions: LF conceived the study, DG and IR carried out field measurements, LF performed the statistical analyses, LF wrote the manuscript, LF, PG, CT, SP, GG and GK reviewed the manuscript.

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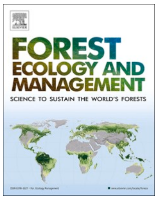

Free behind bars: Effects of browsing exclusion on the growth and regeneration of *Zelkova abelicea*

Laurence Fazan[a], Dany Ghosn[b], Ilektra Remoundou[b], Panagiota Gotsiou[c], Costas Thanos[d], Salvatore Pasta[e], Giuseppe Garfì[e], Gregor Kozlowski[a,f,g,*]

[a] *Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland*
[b] *Department of Geoinformation in Environmental Management – CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100 Chania, Greece*
[c] *Mediterranean Plant Conservation Unit – CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100 Chania, Greece*
[d] *Department of Botany, National and Kapodistrian University of Athens, Panepistimiopolis, 15784 Athens, Greece*
[e] *Institute of Biosciences and BioResources – National Research Council, Corso Calatafimi 414, 90129 Palermo, Italy*
[f] *Natural History Museum Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland*
[g] *Shanghai Chenshan Plant Science Research Center, Chinese Academy of Sciences, Shanghai Chenshan Botanical Garden, 3888 Chenhua Road, Songjiang, 201602 Shanghai, China*

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ABSTRACT

Caprine overbrowsing is a main threat to trees of pastoral mountain woodlands in the Mediterranean region of Europe. In this study, we assess the impact of browsing exclusion on the growth and regeneration of the endangered *Zelkova abelicea*, a Paleogene relict tree endemic to Crete (Greece). Shoot elongation, height growth and natural regeneration were monitored during two to five years in 31 fenced plots across the distribution range of the species. We found that in the absence of browsing pressure, *Z. abelicea* produces shoots on average two times longer than when browsed, therefore clearly demonstrating the negative impact of current browsing pressure on the growth performance of the species. Shoot elongation and height growth were maximal in most plots during the first two years following fencing, after which growth rates decreased. The proportion of trees that reached a height considered out of reach of caprine browsing had more than doubled already after four years, although this was dependent on initial tree height. Shoot elongation and height growth were positively correlated with tree height, and smaller trees took more time to reach a specific height. Seedlings were only found in three fenced plots as well as in two control browsed areas during a single year and only in western Crete. This underlines the possible strong and concerning impact of climatic factors on seed formation as well as on seedling growth and survival, although site specificities such as stand structure and micro-topography should also be considered. Our findings have important implications for conservation actions, as they can help choose which stands and which individuals to fence in priority for efficient long-term conservation.

1. Introduction

Crete has a very long history of browsing. Even before the introduction of domesticated goats in the early Neolithic, a diverse community of wild browsers, e.g. several deer species, a dwarf elephant and a dwarf hippopotamus existed on Crete (Papanastasis, 1998, Rackham and Moody, 1996, Van der Geer et al., 2006). The probable strong browsing pressure induced by these wild browsers led numerous, mainly endemic, plants on Crete to develop specific adaptations to browsing (e.g. spines, unpalatable twigs, prostrate growth habit, high regeneration potential, poisonous compounds) or to shift their ranges to inaccessible places such as cliffs, already before the Neolithic introduction of domestic goats (Papanastasis, 1998, Rackham and Moody, 1996).

Small-sized, long-established and more or less extensive and sustainable pastoralism was carried out during centuries on Crete, shaping the landscape and ecosystems (Hill et al., 1998, Ispikoudis et al., 1999, Kosmas et al., 2015, 2016, Lorent et al., 2009). During the 20th century, due to the socioeconomic changes that shook Europe after the Second World War, pastoralism drastically changed on Crete. Although the number of farms decreased, more intensive practices arose, and the

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* Corresponding author at: Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland.
E-mail addresses: laurence.fazan@unifr.ch (L. Fazan), dghosn@maich.gr (D. Ghosn), hlektra@maich.gr (I. Remoundou), yiota@maich.gr (P. Gotsiou), cthanos@biol.uoa.gr (C. Thanos), salvatore.pasta@ibbr.cnr.it (S. Pasta), giuseppe.garfi@ibbr.cnr.it (G. Garfì), gregor.kozlowski@unifr.ch (G. Kozlowski).

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number of sheep and goats increased almost exponentially, even more so after the adhesion of Greece to the European Union in 1981 and the access to subsidies delivered to farmers per animal (Bauer and Bergmeier, 2011, Hill et al., 1998, Hostert et al., 2003, Ispikoudis et al., 1993, Kizos et al., 2014, Kosmas et al., 2016, Lyrintzis, 1996, Lorent et al., 2009). At the same time, there has been a strong development of roads in the mountains, also supported by European Union subsidies, making remote areas easier to access and to bring bigger flocks (Hill et al., 1998, Hostert et al., 2003). Some sort of traditional transhumance is still practiced nowadays as flocks are moved from lowland overwintering areas to summer mountain pastures in spring. However, these flocks are composed of much more animals, often surpassing the carrying capacity of the local rangelands, and are often left for longer time stretches to roam freely in specific areas from spring to autumn (Ispikoudis et al., 1993). This uncontrolled overstocking, overbrowsing and partial abandonment of transhumance for semi-permanent pastures has led to rapid and intense landscape deterioration in many places in Crete (Ispikoudis et al., 1993, Papanastasis, 1998). Unsustainable browsing and grazing practices are one of the most important causes of landscape degradation on Crete (Kairis et al., 2015). Overbrowsing as well as underbrowsing becomes clearly detrimental to the conservation of local landscapes when occurring over decades (Papanastasis, 1998). It is not the presence of flocks that is detrimental to the Mediterranean landscape and vegetation, but a lack of sustainable management of the flocks themselves in terms of stocking density (i.e. number of animals per surface per time), herd movement, etc. (Papanastasis, 1998). In fact, pastures and rangelands with low and moderate livestock densities are considered as important priority habitats in Europe (Kairis et al., 2015). Overbrowsing occurs when there are not only changes in the local vegetation structure but also a loss of animal productivity (Wilson and Macleod, 1991). In recent times in Crete, research does not point towards less animal productivity when the landscape is degraded due to unsustainable browsing practices. This is due to the fact that oftentimes the dependency to and use of external feed or fodder is increased in order to compensate the loss of vegetation (Kizos et al., 2014, Kosmas et al., 2015, Lorent et al., 2009).

Zelkova abelicea Lam. (Boiss.) (Ulmaceae) is one of three endemic tree species to Crete (Cambria et al., 2019, Médail et al., 2019, Villar et al., 2015). This Paleogene relict is found only in the mountainous regions of the island above 900 m a.s.l. where it grows in places that are rather cool and not too xeric such as north-facing slopes or in and around dolines. The species is also found growing on scree slopes and in or around seasonal riverbeds as well as at high elevations on south-facing slopes. It forms scattered and isolated stands, with *Acer sempervirens* L., *Quercus coccifera* L. and occasionally *Cupressus sempervirens* L. (Bauer and Bergmeier 2011, Egli 1997, Fazan et al., 2012, Goedecke and Bergmeier, 2018, Sarlis, 1987, Søndergaard and Egli, 2006). Most individuals are found in a stunted dwarfed form due to overbrowsing by goats, with multiple stems and very slow growth. Such individuals can survive for centuries under this dwarfed form (Fazan et al., 2012). However, they cannot produce flower nor fruit. Arborescent, up to 15–20 m of height, fruiting individuals are much rarer and represent ca. 5% of all known individuals. Some stands are even composed entirely of dwarfed individuals. The species propagates easily by vegetative root suckers, especially when erosion or disturbance occurs (Egli, 1997, Fazan et al., 2012, Kozlowski et al., 2014, 2018, Søndergaard and Egli, 2006). *Zelkova abelicea* is classified as endangered (EN) on the IUCN Red List (Kozlowski et al., 2012). Unsustainable pastoral activities pose the most important threats to the species. In fact, most populations are found in heavily browsed areas. Overbrowsing by goats as well as trampling by numerous sheep or goats prevent seedlings from establishing and dwarfed individuals from growing tall and fructifying. Climatic and edaphic factors may also play a role in influencing plant growth and seedling establishment (Bauer and Bergmeier, 2011, Egli, 1997, Kozlowski et al., 2012, Sarlis, 1987). Previous studies pointed out that seeds germinate very slowly and need cold stratification for several months and are therefore very sensitive to climate fluctuations as well as climate change (Fournaraki and Thanos, 2002).

Z. abelicea is emblematic of the Cretan mountains, and the largest trees are often found growing next to abandoned shepherd huts. In the past, trees were pollarded and leaves used for forage (Bauer and Bergmeier, 2011, Rackham and Moody, 1996). The wood of *Z. abelicea* was and still is considered the best to make traditional shepherd sticks, i.e. so-called “katsounes”. This practice continues today although it is now illegal because *Z. abelicea* is protected by the Greek State, forbidding the use and collection of any of its parts (Fournaraki and Thanos, 2006, Rackham and Moody, 1996).

Since 2014, a project for the conservation of *Z. abelicea* has been carried out on Crete with different conservation actions (see: www.abelitsia.gr and www.zelkova.ch). One of these actions led to the installation of permanent fenced plots throughout the distribution range of the species, with a complete exclusion of browsing and a yearly monitoring to assess tree growth. In this paper, we 1) investigate the effects of browsing exclusion within these permanent plots during several consecutive years on the growth and regeneration of *Z. abelicea* and 2) compare annual growth within the fenced plots with the growth of *Z. abelicea* in control non-fenced, browsed areas.

2. Material and methods

2.1. Sampling procedure and data collection

Within the scope of the project for the conservation of *Z. abelicea*, 31 plots containing dwarfed *Z. abelicea* individuals were fenced in twelve study areas throughout the whole distribution range of the species (Fig. 1). Only Mount Psiloritis which contains a single known *Z. abelicea* population was not included in the study because no agreement was reached with local land users regarding fencing procedures. The plots were established in order to exclude caprine and ovine browsing and trampling and to allow regrowth of *Z. abelicea* individuals, seedling establishment and development of a non-browsed plant community (Fig. 2A and 2B). Plots were established gradually every autumn between 2014 and 2017, and monitored annually until 2019, leading to two to five years of data collection per plot. Chronology of plot establishment can be found in Table 1. Plots were very diverse in terms of plot surface, number of *Z. abelicea* individuals, initial tree height and altitude (Tables 1 and 4). They are probably also diverse in terms of browsing pressure, however, precise stocking densities, flock composition (i.e. proportion of goats), length of browsing period or browsing history are unknown. The available data for the whole island, without considering seasonal patterns of flock transhumance, show that in 2019, there was a total of 2,301,679 goats and sheep on Crete, of which 23% are goats (ELSTAT, 2021a). This amounts to a total stocking density of 5 animals/ha, or 1.15 goats/ha when considering forest areas and pastures (i.e. 461120 ha, ELSTAT, 2021b). To our knowledge, all of the mountain woodlands composed of *Z. abelicea* trees and shrubs included in this study are important pastures or browsing areas for goats and sheep. Although more precise census data are lacking, they are most likely under strong browsing pressure. Previous studies in other areas of Crete have shown that stocking densities greatly surpass (up to 20 times more) the carrying capacity of the local rangelands (Ispikoudis et al., 1993, Kairis et al., 2015, Kosmas et al., 2016, Lyrintzis 1996, Menjli and Papanastasis, 1995, Papanastasis et al., 2002). The only wild browser of Crete is the agrimi goat (*Capra aegagrus cretica*). The main population of agrimi is found nowadays only in the Levka Ori in western Crete, although individuals were introduced on several satellite islets for conservation purposes (Geskos, 2013, Horwitz & Bar-Gal, 2006). However, its potential impact on *Z. abelicea* is most probably marginal or null compared to that of domestic goats since the estimated agrimi population size on Crete is of ca. 1000 individuals (Geskos, 2020). In every plot, for every *Z. abelicea* individual, the length of the longest shoot (Fig. 2C) produced during the year (hereafter named as shoot length, and possibly

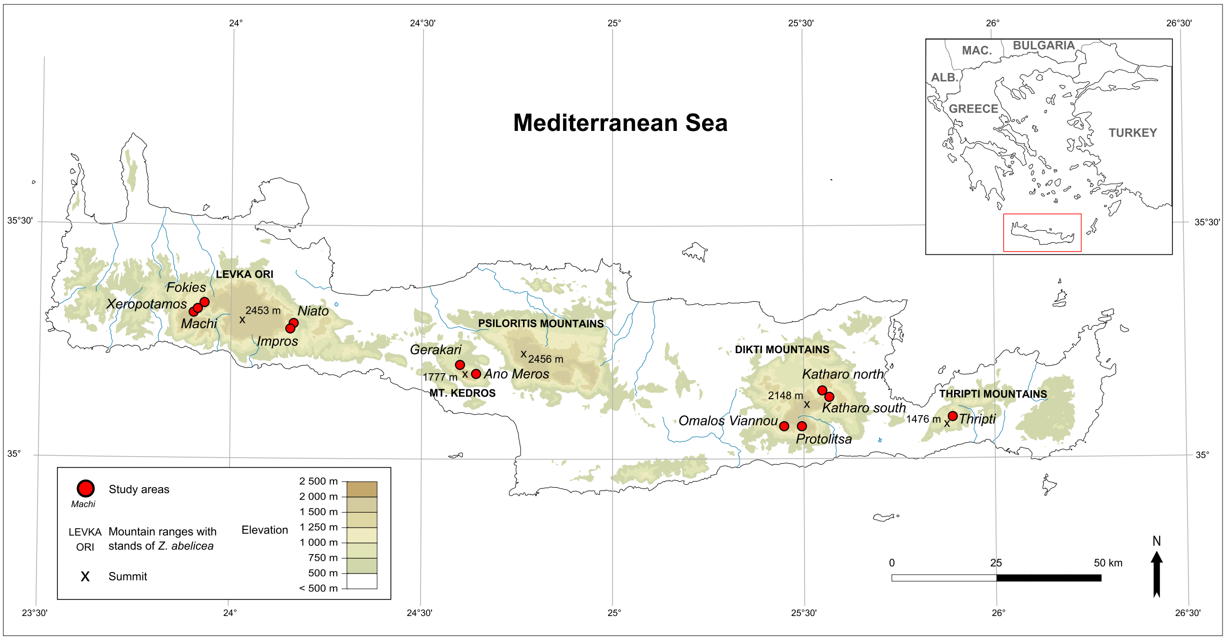

Fig. 1. Location of the study areas in the mountains of Crete (Greece).

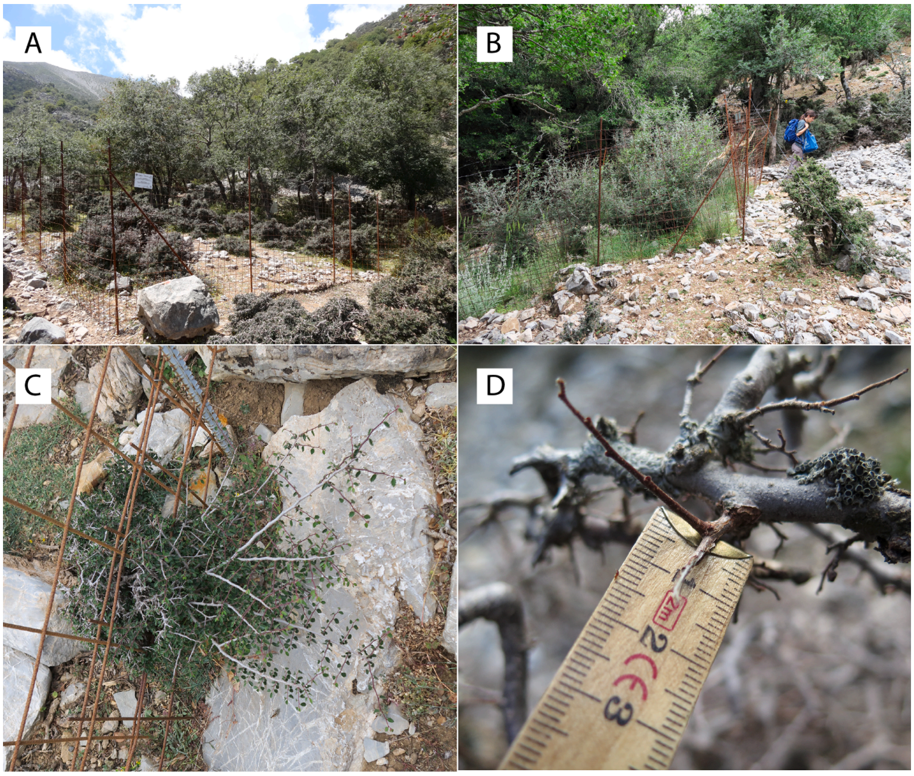

Fig. 2. A. Dwarfed browsed individuals of *Z. abelicea* in the foreground and tree type individuals in the background enclosed within a fenced plot. B. Differences in growth and vegetation inside and outside of a fenced plot four years after fencing. C. Dwarfed *Z. abelicea* producing long non-browsed shoots within a fenced plot (right) but with minute growth in browsed areas outside of the plot (left). D. Annually produced shoots on a browsed *Z. abelicea.*

different from year to year depending on yearly growth) and tree height were monitored from the time the fences were installed (T0), and thereafter every year (T1, T2, etc.) at the end of the growing season in October or November. Shoot length was not measured in T0. Growth parameters were measured with a centimeter measuring stick. For trees higher than 2 m, growth parameters were visually estimated. Additionally, in October 2019, the length of the longest shoot and tree height were also measured in each of the twelve study areas on a total of 120 (10 per area) control non-fenced and subject to browsing *Z. abelicea* individuals (Fig. 2D). These sampled individuals were located in the

Table 1
Characteristics of fenced plots and control non-fenced areas. T0: year of establishment of plot. Nb. of *Z. abelicea* trees: number of individuals with full records. F: fenced, C: control non-fenced. Damage: occurrence of 1st damage: SP: spring, SU: summer, WI: winter. H: human induced. N: natural causes such as rockfall or snow, A: animal influence.

Mountain range		Area	Plot ID	Altitude (m a.s.l.)	T0	Plot size (m^2)	Nb. of Z. *abelicea* trees	F/C	Damage
Levka Ori	West	Xeropotamos	XER1	1270	2014	10	2	F	SP 2017H
			XER2	1220	2014	20	8	F	SP 2017H
			XER3	1243	2014	70	6	F	SU 2016H
			XER	1230	–	–	10	C	–
		Machi	KAL1	1171	2014	25	14	F	–
			KAL2	1195	2014	18	7	F	–
			KAL	1170	–	–	10	C	–
		Fokies	POR1	1071	2014	39	18	F	WI 2015/16N
			POR2	1140	2014	37	7	F	–
			POR	1070	–	–	10	C	–
	East	Niato	NIA1	1220	2014	36	2	F	–
			NIA2	1219	2014	32	5	F	–
			NIA3	1211	2014	21	3	F	–
			NIA4	1221	2014	19	3	F	–
			NIA	1215	–	–	10	C	–
		Impros	IMB1	1178	2015	34	24	F	–
			IMB2	1172	2015	21	8	F	–
			IMB3	1178	2015	21	11	F	–
			IMB	1178	–	–	10	C	–
Kedros		Gerakari	GER1	1255	2015	33	9	F	–
			GER2	1257	2015	26	7	F	SU 2016A
			GER	1255	–	–	10	C	–
		Ano Meros	ANME1	998	2015	12	1	F	SU 2016N
			ANME2	986	2015	37	7	F	–
			ANME	995	–	–	10	C	–
Dikti	North	Katharo north	KATH1	1177	2016	38	14	F	–
			KATH2	1201	2016	67	27	F	–
			KATH12	1200	–	–	10	C	–
		Katharo south	KATH3	1149	2016	24	7	F	WI 2016/17H
			KATH4	1153	2016	59	6	F	–
			KATH34	1150	–	–	10	C	–
	South	Omalos Viannou	VIAN1	1324	2015	23	3	F	–
			VIAN2	1327	2015	22	10	F	–
			VIAN3	1309	2015	15	8	F	–
			VIAN	1325	–	–	10	C	–
		Protolitsa	PROT1	1637	2015	19	11	F	–
			PROT2	1619	2015	20	14	F	–
			PROT3	1593	2015	19	6	F	–
			PROT	1620	–	–	10	C	–
Thripti		Thripti	THR1	1152	2017	95	19	F	–
			THR2	1152	2017	88	28	F	–
			THR3	1155	2017	105	25	F	–
			THR	1154	–	–	10	C	–

immediate vicinity (<30 m of distance) of the fenced plots.

Natural regeneration of *Z. abelicea,* sexually through seedlings or vegetatively through root suckers, was also monitored in every plot and external area every spring between 2015 and 2019. Seedling and root sucker presence and number were recorded and counted.

2.2. *Selection of fenced plots and trees for analysis*

Disturbances such as intentional or nature-induced destruction of fences with subsequent browsing occurred in seven plots at different times (Table 1). Such plots were excluded from further analyses unless mentioned otherwise. Moreover, for some trees, measurements were missing for one or several years, either because the individual was erroneously not measured, died or was not previously noticed. Such trees were also excluded from further analyses. Therefore, a total of 271 trees with full records (or 320 when also counting the 49 trees with full records included in the disturbed plots) found within the fenced plots were analyzed. Plots contained on average 10 *Z. abelicea* individuals, but with a wide range between one and 28 trees (Table 1).

2.3. *Analyses*

Statistical analyses were carried out using R (R Core Team, 2020, version 4.0.2.). Average shoot length, tree height and annual height change and standard deviations were computed. Significance in differences in shoot length between fenced plots and control non-fenced areas were assessed using a Wilcoxon rank sum test (wilcox.test, package stats, Hollander and Wolfe, 1973) for 2019, the only year for which data were available for the control non-fenced plots. Correlations between shoot length and time after fencing as well as for height growth and time after fencing were done using Spearman's rank correlation (cor.test, package stats, Hollander and Wolfe, 1973) in order to show the general direction of shoot or height changes depending on time. Further correlations were made between shoot length, tree height and height changes also using Spearman's rank correlation. The browsing height that goats can reach strongly varies amongst authors with a range of heights between one and two meters depending on goat variety, whether or not bipedal browsing (i.e. rise up on hind legs) was considered, and vegetation type, i.e. dense growing or large shrubs are more difficult to browse up high unless they can be climbed upon (e.g. Foroughbakhch et al., 2013, Harrington, 1979, Nastis, 1997, Ouédraogo-Koné et al., 2006, Platis and Papanastasis, 2003, Sanon et al., 2007, Skarpe et al., 2007, Webb et al., 2004).

In the present study, *Z. abelicea* individuals measuring > 200 cm are considered as being tall enough to escape browsing. Although browsing probably sporadically occurs above that height, we consider such individuals as having a strong likelihood of escaping browsing based on our field observations and browsing height thresholds given in the literature cited above.

3. Results

3.1. Shoot lengths

Shoot lengths per time in non-disturbed fenced plots as well as in control non-fenced areas are given in Table 2 and Fig. 3, while individual plot data are found in Appendix A, Table A.1 and Fig. A.1. In 2019 (only year for which data is available for both the control unfenced plots and fenced plots) shoots in undisturbed fenced plots were on average 1.85 times longer than shoots in control non-fenced areas, with values varying between 1.10 and 4.10 times longer, depending on locality. Shoot length is significantly ($p < 0.1$) longer in non-disturbed fenced plots compared to control non-fenced areas in 2019 for most plots, except for three plots (Table 3). Correlations between shoot length and increasing time after fencing are also found in Table 3. Overall in non-disturbed fenced plots, there is no significant correlation (rho: −0.02, $p > 0.1$) between shoot lengths and time after fencing. However, when considered individually, for a majority (12 plots) of non-disturbed plots there is a significant ($p < 0.1$) and mostly strong negative correlation between shoot length and increasing time after fencing, while six plots show negative but non-significant correlations. Only six plots show positive trends but only two are significant ($p < 0.1$). Shoot length was positively correlated with tree height (rho: 0.54, p-value < 0.001), with taller trees generally producing longer shoots.

3.2. Height changes

Average tree height and height changes per time for non-disturbed fenced plots as well as for control non-fenced areas are found in Table 2. Trees in fenced plots had heights in T0 comprised between 6 and 330 cm, whereas trees in control non-fenced areas measured between 20 and 175 cm. Strong variations occurred between trees in terms of height change, as the highest annual growth change amounted to 80 cm while the minimum was 0 cm. Table 4 and Fig. A.2 in Appendix A give detailed results for every fenced plot. In 2019 at the end of the study period, trees had on average grown 34.36 ± 30.80 cm with variations between 0 and 148 cm depending on individual tree. Height changes were overall not significantly correlated with time after fencing (similarly to shoot lengths) (rho: 0.02, $p > 0.1$). However, when fenced plots were considered individually, height changes were negatively correlated with time after fencing in a majority of (non-disturbed) plots, either significantly ($p < 0.1$) for 12 plots or not significantly ($p > 0.1$) in four plots (Table 4). Significant ($p < 0.1$) positive values were found in one single plot, while the remaining seven plots have positive but not significant ($p > 0.1$) values (Table 4). In addition, height changes were positively correlated with tree height (rho: 0.44, p-value < 0.001) showing that taller trees had a tendency to grow more per year.

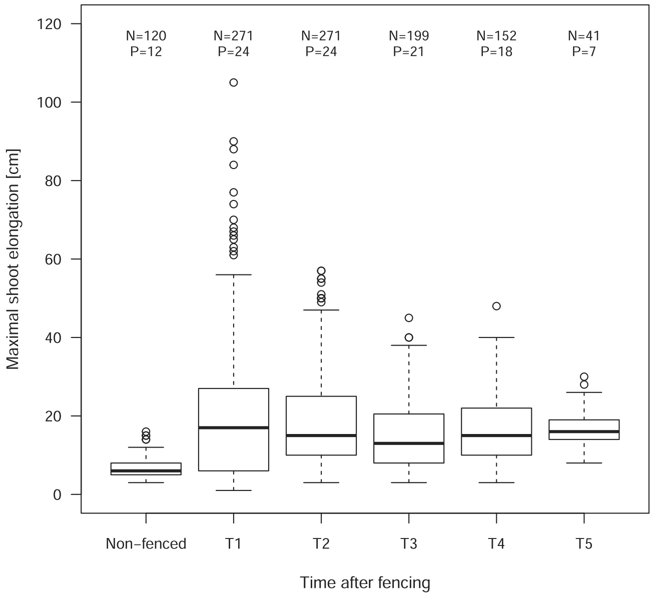

Fig. 3. Shoot length in non-disturbed fenced plots one to five years after fencing (T1 to T5) and in control non-fenced areas. N: number of trees, P: number of fenced plots or control non-fenced areas.

The percentage of trees in T0 (in non-disturbed plots) that reached the 200 cm threshold at which the browsing likelihood is considered low was 4%, although strong variations (0–43%) between plots exist (Table 4). In 2019 (i.e. plots having been fenced two (T2) to five (T5) years depending on locality), at the end of the study, 10% of trees (in non-disturbed plots) measured > 200 cm, with strong variations (0–67%) amongst plots (Table 4).

3.3. Homogenous number of trees through time

The number of plots per time varied (i.e. 24 plots in T1, but only 7 plots in T5) due to the fact that the plots were established gradually between 2014 and 2017. This non-homogeneous number of plots through time may influence also our results. Therefore, we made the same analyses of shoot length and height changes over a homogeneous dataset including only plots that had complete data from T1 to T4 (18 plots, 151 trees). We found similar results (Table 5) to those obtained when including all non-disturbed plots over the whole five year of the study. Indeed, shoot length here was also maximal during the first and/or second year after fencing after which it decreased (Appendix A, Fig. A.3). Average height and height changes per time are also given in Table 5: after four years of fencing, trees had grown on average 45.32 cm (range: 0–140 cm). The percentage of trees in T0 that measured >200 cm was 6%. In T1 it amounted to 10%, in T2 it rose to 11%, in T3 it

Table 2

Growth characteristics per time for non-disturbed fenced plots and control non-fenced areas. Average, minimum and maximum shoot lengths, average tree height and height change and number of plots and trees are given.

Fencing	Time	Shoot length (cm)			Height (cm)		Nb plots	Nb trees
		Average	Min	Max	Average	Change		
Fenced	T0	–	–	–	78.40 ± 54.84	–	24	271
	T1	20.61 ± 17.92	1	105	88.73 ± 58.24	10.33 ± 12.16	24	271
	T2	18.58 ± 12.38	3	57	99.81 ± 61.69	11.08 ± 10.23	24	271
	T3	15.41 ± 8.86	3	45	124.31 ± 65.89	9.63 ± 8.91	21	199
	T4	16.46 ± 8.28	3	48	131.65 ± 73.34	7.82 ± 6.60	18	152
	T5	17.24 ± 4.54	8	30	200.22 ± 58.10	9.83 ± 4.23	7	41
Non-fenced	–	6.83 ± 2.65	3	16	83.14 ± 37.34	–	12	120

Table 3
Levels of significance of Wilcoxon rank sum test between shoot length in fenced plots and control non-fenced areas in 2019. Spearman's rank correlation rho between shoot length and time after fencing with significance levels are also given. Levels of significance: *** $p < 0.001$, ** $p < 0.01$, *$p < 0.1$. [d] plots in which disturbance occurred.

Fenced	Non-fenced	T2	T3	T4	T5	Rho
XER1[d]	XER	–	–	–	*[d]	−0.56[d] *
XER2[d]	XER	–	–	–	***[d]	−0.75[d] ***
XER3[d]	XER	–	–	–	***[d]	−0.41[d] ***
KAL1	KAL	–	–	–	***	−0.80***
KAL2	KAL	–	–	–	***	−0.92***
POR1[d]	POR	–	–	–	***[d]	−0.55[d] ***
POR2	POR	–	–	–	***	−0.75***
NIA1	NIA	–	–	–	*	0.12
NIA2	NIA	–	–	–	**	−0.29
NIA3	NIA	–	–	–	0.61	−0.48*
NIA4	NIA	–	–	–	*	−0.43
IMB1	IMB	–	–	**	–	−0.06
IMB2	IMB	–	–	***	–	−0.47**
IMB3	IMB	–	–	***	–	−0.53***
GER1	GER	–	–	***	–	−0.44**
GER2[d]	GER	–	–	0.52[d]	–	−0.46[d] ***
ANME1 [d]	ANME	–	–	0.14[d]	–	−1[d]
ANME2	ANME	–	–	***	–	0.23
VIAN1	VIAN	–	–	**	–	−0.51*
VIAN2	VIAN	–	–	***	–	−0.52***
VIAN3	VIAN	–	–	*	–	0.45**
PROT1	PROT	–	–	***	–	−0.06
PROT2	PROT	–	–	**	–	0.03
PROT3	PROT	–	–	0.96	–	−0.09
KATH1	KATH12	–	***	–	–	0.28*
KATH2	KATH12	–	***	–	–	−0.63***
KATH3 [d]	KATH34	–	**[d]	–	–	−0.27[d]
KATH4	KATH34	–	**	–	–	−0.76***
THR1	THR	**	–	–	–	−0.32*
THR2	THR	0.53	–	–	–	0.05
THR3	THR	***	–	–	–	−0.20

reached 13% and in T4, 15% of individuals were over 200 cm.

3.4. Fenced plots with disturbance

Disturbances, with recorded signs of subsequent browsing, occurred in 7 fenced plots at different times after establishment of the fences (Table 1). Despite these disturbances, shoot lengths were significantly ($p < 0.1$) longer in XER1, XER2, XER3, POR1 and KATH3 plots compared to control external plots in 2019 and a significant ($p < 0.1$) negative correlation between shoot length and time after fencing was also visible for four of these five plots, and only not significant ($p > 0.1$) for KATH3. Both GER2 and ANME1 have shoot lengths that are not significantly ($p > 0.1$) longer than shoots in browsed areas, although both show a negative correlation between shoot length and passing time, but significant ($p < 0.1$) only for GER2 (Table 3 and Appendix A, Fig. A.1). Average height changes between T0 and the last year of measurement were positive for all of the disturbed plots, although some individual trees showed negative values (i.e. they were smaller than in T0) in XER1, XER3 and GER2 (Table 4). Correlation between height growth changes and time after fencing were significant ($p < 0.1$) and negative only for POR1. For all other plots they were non-significant, either negative (XER1, XER2) or positive (XER3, GER2, ANME1, KATH3). The proportion of trees that reached 200 cm during the last year of measurement was either similar to T0 and had not changed (POR1, ANME1, KATH3) or had increased (XER1, XER2, XER3, GER2).

3.5. Natural regeneration

In 2018, two, three and twenty seedlings were found in three fenced plots (KAL2, XER2 and XER3, respectively), in open areas or under shrub cover and three and thirty seedlings were found in two external areas (KAL and XER, respectively). Seedlings were found mainly, but not exclusively, growing under shrubs or in between loose rocks, only in Machi and Xeropotamos in western Crete, but none were found to have survived in 2019. Although no new seedlings were recorded in 2019 within the study sites, the presence of new seedlings was noted from adjacent areas to the above-mentioned study sites. No new vegetatively propagated (suckers) individuals were recorded within the studied sites.

4. Discussion

Goats are known to reduce or limit woody plants or tree growth (Bashan and Bar-Massada 2017, Elias and Tischew 2016, Gizicki et al., 2018, Hester et al., 2006, Maděra et al., 2019, Mancilla-Leytón et al., 2013, Rooke 2003). In our study, we clearly show that this was also the case here. *Z. abelicea* individuals in fenced plots where browsing was excluded produced significantly (on average two times) longer shoots than individuals in areas where browsing occurred. Furthermore, in some plots, some trees grew over 100 cm in height since they were fenced (Table 4), showing the potential of the species to grow when given the opportunity. This unambiguously demonstrates the strong impact that current browsing has on the growth of *Z. abelicea* in the Cretan mountains. Most plots showed a maximal shoot elongation and height growth during the first two years after browsing exclusion, with stronger growth variations between individuals within the first year compared to the second. Subsequent years involved less growth, while staying high. The reasons behind this phenomenon are still unclear and could be linked with tree physiology or energy reserves, and we do not yet have sufficient perspective to see if this trend will continue with passing years. Tsiourlis (1998) found that *Q. coccifera* produced more biomass the first year after browsing exclusion, with decreasing values thereafter and a possible stabilization after the third year, although the study did not include subsequent years to validate this assumption. Konstantinidis et al. (2005) observed that *Q. coccifera* produced longer shoots in the first two years after a fire event and then has a slower growth. In burnt shrubs, this increased growth during the first few years after disturbance is due to the mobilization of energy reserves (Bowen and Pate, 1993).

It is possible that a similar phenomenon happens when *Z. abelicea* is not browsed anymore. However, the removal of browsing is not a trigger event similar to fire, except if we consider the absence of browsing or browsing induced chemical reactions as being a trigger. Moreover, since the plots were fenced at different times over the course of four separate years, such a reaction can most probably not be imputed to interannual climatic fluctuations. It is not impossible that this pattern could be linked to the way sampling was done, since shoot length was always measured on the longest annually produced shoot and thus not always on the same shoot, although the fact that this pattern seems to happen throughout most plots and over several years tends to exclude this hypothesis.

As the large standard deviations clearly point out, shoot lengths within the fenced plots were much more variable than in the control non-fenced areas. Height changes and shoot lengths were also more variable the first year after fencing than in subsequent years. This points towards the fact that in browsed areas, growth is mainly regulated by browsing pressure (Fazan et al., 2012), whereas in fenced plots where browsing is not a limiting factor anymore, other factors either specific to the tree or to the site (e.g. tree height, energy reserves, micro-climate, soil, resource competition, etc.) may play a major role and individual trees and plots show a wide range of variability to browsing removal.

In addition, we demonstrate that protection against browsing over several consecutive years allows prostrate, shrubby dwarfed *Z. abelicea* individuals to grow enough to reach a height considered as sufficient to escape most browsing by goats. Although this strongly depends on the initial height of the individuals and the growth rate of their shoots, the number of trees taller than 200 cm was 2.5 times larger already after 4 years of fencing, while in some specific plots (e.g. KAL1, KAL2, NIA3,

Table 4
Average (with standard deviation), minimum and maximum height changes between T0 and the last time of measurement (Tx) for every fenced plot. Proportion of trees higher than 200 cm in T0 and Tx. Spearman's rank correlation rho between height change and time after fencing with significance levels are also given. Levels of significance: *** $p < 0.001$, ** $p < 0.01$, *$p < 0.1$. Average height (with standard deviation) at T0 when the plot was established. Last time of measurement (Tx). ^{d} plots in which disturbance occurred.

Plot	Height change T0-Tx (cm)			Prop trees > 200 cm		Rho	Height at T0 (cm)	Tx
	Mean	Min	Max	T0	Tx			
XER1^{d}	35.50 ± 29.0^{d}	−56^{d}	55^{d}	0.00	0.50	−0.36^{d}	143 ± 10	T5
XER2^{d}	72.88 ± 53.0^{d}	24^{d}	91^{d}	0.00	0.25	−0.31^{d}	92 ± 50	T5
XER3^{d}	17.79 ± 20.6^{d}	−6^{d}	87^{d}	0.00	0.05	0.00^{d}	92 ± 43	T5
KAL1	96.21 ± 19.0	64	122	0.14	0.57	−0.28*	126 ± 65	T5
KAL2	96.14 ± 24.9	64	134	0.00	0.57	−0.31*	126 ± 49	T5
POR1^{d}	58.63 ± 27.3^{d}	11^{d}	118^{d}	0.00	0.00	−0.33^{d} ***	59 ± 21	T5
POR2	74.57 ± 21.2	43	95	0.00	0.00	−0.31*	62 ± 23	T5
NIA1	54.00 ± 19.8	40	68	0.00	0.00	0.31	131 ± 21	T5
NIA2	69.80 ± 15.4	53	86	0.00	0.20	−0.41*	118 ± 38	T5
NIA3	48.33 ± 32.1	12	73	0.33	0.67	0.20	186 ± 98	T5
NIA4	91.00 ± 54.2	40	148	0.33	0.67	−0.74**	101 ± 96	T5
IMB1	15.67 ± 12.9	0	47	0.00	0.00	0.02	39 ± 25	T4
IMB2	57.25 ± 15.4	28	78	0.00	0.00	−0.68***	76 ± 16	T4
IMB3	66.00 ± 16.8	22	85	0.00	0.00	−0.73***	59 ± 17	T4
GER1	69.30 ± 16.2	38	90	0.11	0.33	−0.35*	118 ± 67	T4
GER2^{d}	5.44 ± 7.80^{d}	−3^{d}	18^{d}	0.33	0.43	0.07^{d}	156 ± 77	T4
ANME1^{d}	8.00 ± 0.00^{d}	8^{d}	8^{d}	0.00	0.00	0.77^{d}	175 ± 0	T4
ANME2	36.29 ± 43.3	0	108	0.43	0.57	0.16	177 ± 84	T4
KATH1	13.00 ± 5.1	6	23	0.07	0.07	0.25	111 ± 50	T3
KATH2	25.67 ± 8.4	5	41	0.00	0.04	−0.36***	87 ± 38	T3
KATH3^{d}	26.86 ± 7.93^{d}	20^{d}	42^{d}	0.00	0.00	0.10^{d}	70 ± 29	T3
KATH4	40.83 ± 8.1	31	50	0.17	0.17	−0.66**	146 ± 35	T3
VIAN1	77.67 ± 7.0	71	85	0.00	0.00	−0.74**	86 ± 40	T4
VIAN2	35.30 ± 12.3	15	57	0.00	0.00	−0.10	78 ± 40	T4
VIAN3	13.50 ± 4.2	9	22	0.00	0.00	−0.29	54 ± 41	T4
PROT1	30.36 ± 9.3	14	48	0.09	0.09	0.04	99 ± 83	T4
PROT2	15.43 ± 11.8	0	38	0.00	0.00	0.16	62 ± 30	T4
PROT3	28.17 ± 6.6	18	36	0.00	0.00	0.45*	73 ± 37	T4
THR1	19.16 ± 10.9	1	42	0.00	0.00	−0.19	64 ± 40	T2
THR2	6.71 ± 6.7	0	28	0.00	0.00	0.38**	41 ± 17	T2
THR3	14.88 ± 9.1	3	37	0.00	0.00	−0.15	38 ± 13	T2

Table 5
Growth characteristics per time for the 151 trees in 18 fenced plots with homogenous data from T1 to T4. Average shoot length, average tree height and height change are given.

Time	Average shoot length (cm)	Height (cm)	
		Average	Change
T0	–	86.74 ± 60.78	–
T1	25.03 ± 21.26	98.99 ± 63.82	12.25 ± 14.72
T2	24.03 ± 13.82	113.61 ± 67.19	14.62 ± 12.22
T3	17.15 ± 9.31	124.19 ± 70.51	10.58 ± 9.39
T4	16.51 ± 8.29	132.06 ± 73.41	7.87 ± 6.60

NIA4, ANME2), over 50% of individuals had reached that height at the end of the study period in 2019. These findings are highly important for conservation practitioners or rangeland managers, as they can help to estimate how many years will be needed to reach a sufficient height depending on tree size and locality, or which stands to select in priority to reach a desired height the quickest possible. In addition, it is crucial for the natural regeneration through seed of *Z. abelicea* for trees to reach a height at which flowering and fruiting branches are out of reach of goats. Indeed, overbrowsed individuals do not produce flowering shoots (Kozlowski et al., 2014). Increasing the number of potentially fruiting trees will in turn increase the number of fruit produced and thus improve the chances of natural regeneration through seedlings.

Most plots in which disturbance (i.e. browsing by goats after fencing) occurred showed an increase in average shoot length despite browsing. Only in two plots (GER2 and ANME1) shoot lengths were not significantly different from shoots in browsed areas (Table 3). However, it is difficult to assess if the non-significant shoot elongations within these disturbed plots are a consequence of a browsing disturbance or due to tree or site-specific characteristics (e.g. micro-climate, soil, competition, energy reserves, etc.). Height increased in all of the plots with disturbance between T0 and the last time they were measured, although in three plots (XER1, XER3, GER2), some individuals lost height (Table 4), indicating that browsing damage surpassed tree growth. The negative correlation of shoot growth and height change with time after fencing was also not as clear in disturbed fenced plots compared to undisturbed fenced plots.

In undisturbed fenced plots, shoot and height elongation were positively correlated with tree height and were found to be very different amongst sites. There seems to be important growth differences (both in terms of shoot length and height change) between plots. Some of these variations are probably imputable to the fact that individuals within the plots have different initial heights, or to the fact that individual *Z. abelicea* trees could possibly react differently to browsing removal depending on their age, energy reserves, competition, etc. However, some plots showed very slow growth (i.e. NIA1, ANME2, VIAN3, PROT2, PROT3 and THR2 in T1, VIAN3 and THR2 in T2, NIA4 and PROT2 in T3, PROT3 in T4 and NIA3 in T5), with no significant differences with the control non-fenced areas, unlike the majority of plots. Further investigations should be carried out to see if these differences and slow growth rates are due to differences in initial tree height or spatial structure of plant communities (i.e. does tree density or competition influence growth rates?), location (i.e. to what extent do geographical parameters such as climate, soil chemical and physical properties or altitude influence growth?) or past browsing pressure (i.e. stocking rate and seasonality of browsing) and flock composition (goats vs. sheep ratio).

The rarity of natural regeneration through seedling recruitment both in fenced plots and control unfenced plots in most years and sites can be regarded as concerning. This phenomenon was already noticed by Egli

(1997) both in fenced unbrowsed as well as browsed areas. The impact of browsing domesticated flocks has very often been regarded as a crucial negative factor hampering tree seedling establishment in Mediterranean habitats, and with this respect, the facilitating role of shrub cover has been largely recognized. Several studies (e.g. Baraza et al., 2006, Di Pasquale and Garfì, 1998, Tiscar-Oliver, 2015), have clearly demonstrated that thorny or unpalatable shrubs can act as physical barriers protecting seedlings and saplings from herbivory and trampling. Moreover, the role of shrub cover on seedling establishment and growth can be diverse and complex by providing a favorable micro-habitat against extreme solar irradiation, photo-inhibition and desiccation (Castro et al., 2004, Rodríguez-García et al., 2011, Rühl et al., 2006, Tiscar-Oliver, 2015). In our study, we did not focus specifically on the interactions between *Z. abelicea* and shrub cover. However, we did observe that seedlings in fenced plots were found both in open gaps and under shrub cover, whereas in external, browsed areas most seedlings were found in more protected locations, such as below the canopy of the neighboring shrubs or in between loose rocks, and were absent from more open areas probably due to herbivory. Furthermore, since in our study, seedlings were also found in external areas, the absence of recruitment through seedlings cannot be solely imputed to over-browsing. Indeed, the absence of seedlings in all sites and years except for three fenced and two control areas in 2018 and adjacent areas in 2019 in western Crete points towards a strong influence of some other factor on seedling survival, or seed soundness, regardless of the browsing status. We hypothesize that climatic conditions possibly play an important role in *Z. abelicea* seedling survival alongside browsing pressure, as was already noted by Egli (1997). Fruit production in *Z. abelicea* as well as the proportion of fruits containing a viable embryo seem to strongly fluctuate depending on the year and site (personal observations, Egli, 1997, Fournaraki and Thanos, 2002, 2006, Søndergaard and Egli, 2006), which in turn will influence the presence of seedlings. In addition, one must also consider site specificities (e.g. micro-topography or stand structure and dynamics) that could influence the occurrence and survival of seedlings. Some of the studied sites (e.g. Thripti) are characterized by the absence of individuals above 2 m (i.e. that are able to produce fruit), whereas others (e.g. Protolitsa) have fruiting individuals but are found on steep stony slopes unfavorable to soil retention and the establishment of seedlings. The fact that no surviving seedlings were found again in 2019, even in the fenced plots, and that seedlings were not found in any other site raises concern for the long-term conservation and genetic diversity of the species. Furthermore, no new suckers were found in our study. However, this is not surprising since suckering appears mostly after disturbance events affecting roots such as fire or erosion (Egli, 1997, Fazan et al., 2012). Thanks to its capacity to profusely re-sprout through root suckers after disturbance events, *Z. abelicea* can propagate and survive asexually in the absence of naturally produced seedlings, but the genetic diversity will be impoverished.

With the *Z. abelicea* conservation project, it is the first time that so many areas containing *Z. abelicea* individuals and spread out through most of the distribution area of the species were fenced, and for such a long span of time. At the time of submission of this article, the oldest plots have been fenced for 6 consecutive years. Although some plots did suffer from anthropogenic disturbances, most did not, and this success can be imputed to the small size of the fenced plots, and more importantly, to the involvement and information of local people in and about the *Zelkova* project, a crucial prerequisite for success in conservation projects (Tisdell, 1995, Elbroch et al., 2011).

5. Conclusions

This study shows the strong impact of current browsing pressure on the growth of *Z. abelicea* in the mountains of Crete (Greece). Both shoot length and height clearly increased when browsing was removed. Shoots were on average two times longer in fenced plots than in browsed areas. Interestingly, growth was maximal during the first two years after fencing, and was lower in subsequent years. Although growth rates strongly depended on initial tree height, the proportion of trees that had reached a height considered sufficient to escape browsing had more than doubled after four years of fencing. Natural regeneration through seedlings was found in the study sites only for one year and localized in two specific areas in western Crete and raises concerns about the influence of climatic variables on seed production, viability and seedling survival. Spatial differences in natural regeneration as well as in growth seem to exist between plots and should be further investigated. Our results have important conservation implications and can be used in the future in order to choose which *Z. abelicea* stands to protect in priority depending on conservation goals and available time.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

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Supplementary material

Table A.1. Average annual shoot length ± standard deviation for every fenced plot and external area for every time (T1, T2, etc.). [d] plots and times in which perturbation occurred. [1] only non-disturbed plots.

	Plot	Shoot length (cm)					
		T1	T2	T3	T4	T5	Average
Fenced	XER1[d]	45.5±20.5	24.0±8.5	15.5±3.5[d]	25.0±1.4[d]	17.0±2.8[d]	25.4±13.6
	XER2[d]	49.8±11.4	36.4±5.3	NA	36.8±10.5[d]	23.6±3.8[d]	36.6±12.3
	XER3[d]	43.0±19.9	NA	21.5±10.3[d]	32.7±12.1[d]	22.7±6.9[d]	32.7±16.9
	KAL1	60.6±14.9	34.6±8.4	32.9±6.4	27.1±8.4	18.4±4.3	34.7±16.8
	KAL2	70.6±20.7	43.3±7.9	30.4±8.3	26.6±6.4	13.6±1.6	36.9±22.2
	POR1[d]	38.0±18.7[d]	27.2±11.2[d]	19.6±7.0[d]	20.1±7.0[d]	17.6±6.8[d]	26.0±14.3
	POR2	36.1±8.7	26.1±10.0	18.0±3.6	19.9±3.5	14.7±1.3	23.0±9.7
	NIA1	14.0±8.5	21.0±5.7	17.5±2.1	28.0±7.1	17.5±2.1	19.6±6.6
	NIA2	47.2±22.3	20.8±4.3	19.2±2.3	27.8±5.9	22.2±4.6	27.4±14.4
	NIA3	24.0±14.4	34.7±10.8	19.7±6.4	23.0±4.4	12.7±4.2	22.8±10.6
	NIA4	33.3±12.6	36.7±4.2	14.3±4.0	19.0±7.0	22.7±2.1	25.2±10.6
	IMB1	10.5±6.2	10.8±5.4	10.1±6.0	9.0±3.4	-	10.1±5.4
	IMB2	26.0±9.0	31.0±8.2	21.4±4.3	18.8±3.5	-	24.3±7.9
	IMB3	32.1±11.5	33.2±6.5	19.0±3.5	22.6±3.0	-	26.7±9.1
	GER1	24.8±7.4	45.8±10.6	23.6±4.9	18.3±3.7	-	28.1±12.6
	GER2[d]	12.5±0.7[d]	NA	9.2±3.4[d]	11.0±4.4[d]	-	10.5±3.7
	ANME1[d]	NA	70.0±0.0[d]	35.0±0.0[d]	16.0±0.0[d]	-	40.3±27.4
	ANME2	14.3±11.4	27.1±19.1	23.7±10.0	20.0±6.5	-	21.3±12.9
	KATH1	5.4±2.4	8.2±4.1	6.8±1.3	-	-	6.8±3.0
	KATH2	19.6±8.1	14.7±3.4	10.3±2.9	-	-	14.9±6.5
	KATH3[d]	19.6±11.0[d]	17.6±5.4[d]	14.1±4.5[d]	-	-	17.1±7.5
	KATH4	24.0±1.8	16.8±3.4	15.8±3.2	-	-	18.9±4.6
	VIAN1	29.7±11.7	29.7±6.4	22.7±3.5	20.7±4.2	-	25.7±7.5
	VIAN2	21.2±8.2	18.5±4.1	12.1±4.3	13.9±2.9	-	16.4±6.2
	VIAN3	7.1±6.5	5.3±2.4	7.5±1.6	8.3±2.4	-	7.0±3.7
	PROT1	10.6±4.2	21.4±8.8	12.7±4.2	12.2±1.2	-	14.2±6.7
	PROT2	6.7±2.7	14.5±6.4	7.4±2.4	8.2±2.2	-	9.2±4.9
	PROT3	8.5±4.7	13.3±6.0	12.3±1.2	6.8±3.1	-	10.3±4.7
	THR1	20.5±12.9	12.1±4.4	-	-	-	16.3±10.4
	THR2	8.8±6.6	7.6±3.5	-	-	-	8.2±5.2
	THR3	16.6±9.4	13.6±3.1	-	-	-	15.1±7.1
	Average[1]	20.6±17.9	18.6±12.4	15.4±8.9	16.5±8.3	17.2±4.5	18.1±13.0
Non-fenced	XER	-	-	-	-	-	9.3±2.2
	KAL	-	-	-	-	-	5.3±1.4
	POR	-	-	-	-	-	5.2±0.6
	NIA	-	-	-	-	-	11.2±3.3
	IMB	-	-	-	-	-	5.5±0.7
	GER	-	-	-	-	-	9.3±3.0
	ANME	-	-	-	-	-	7.9±1.7
	KATH12	-	-	-	-	-	3.8±0.8
	KATH34	-	-	-	-	-	6.5±1.4
	VIAN	-	-	-	-	-	5.4±1.1
	PROT	-	-	-	-	-	6.2±0.8
	THR	-	-	-	-	-	6.4±1.2
	Average						6.8±2.7

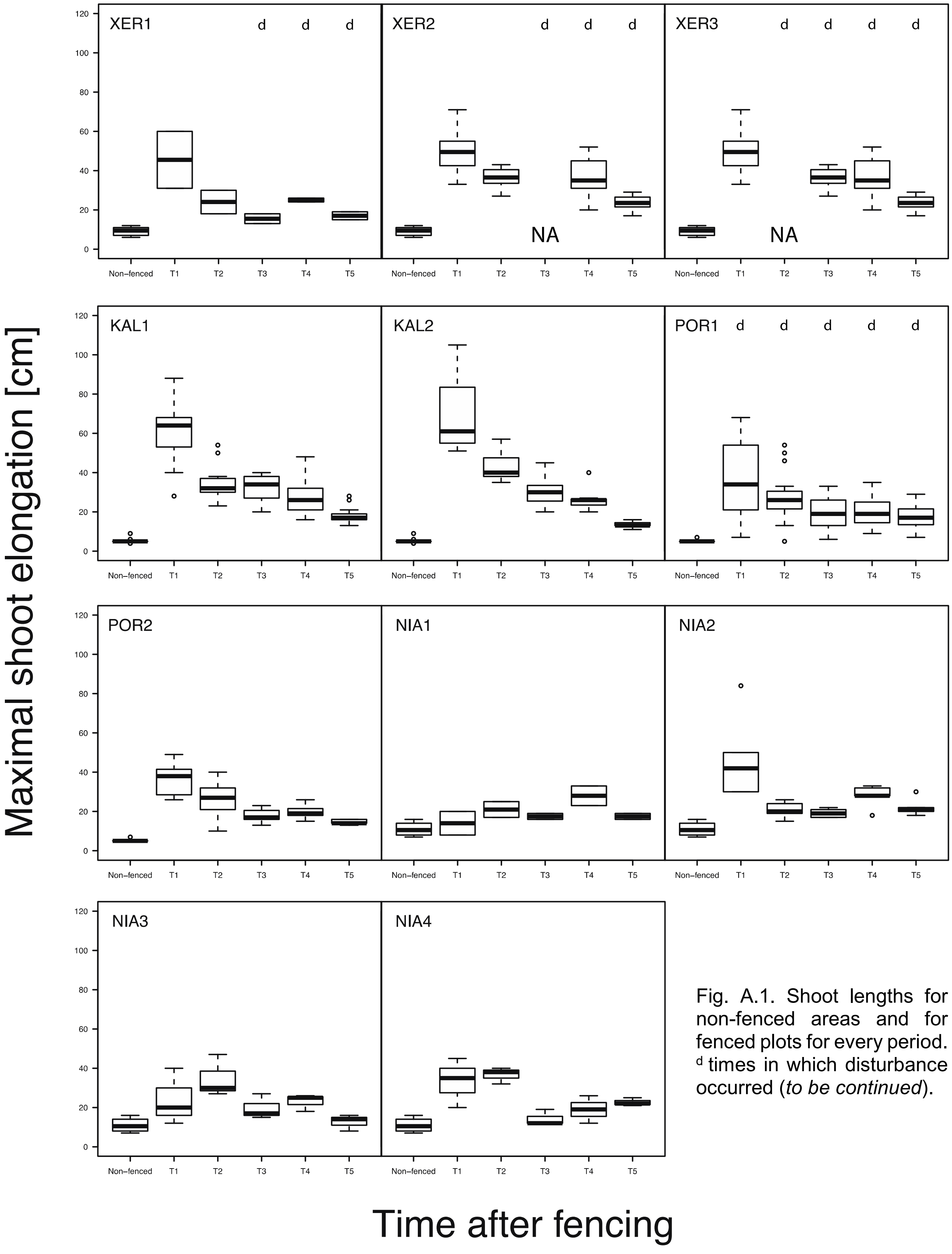

Fig. A.1. Shoot lengths for non-fenced areas and for fenced plots for every period. ^{d} times in which disturbance occurred (*to be continued*).

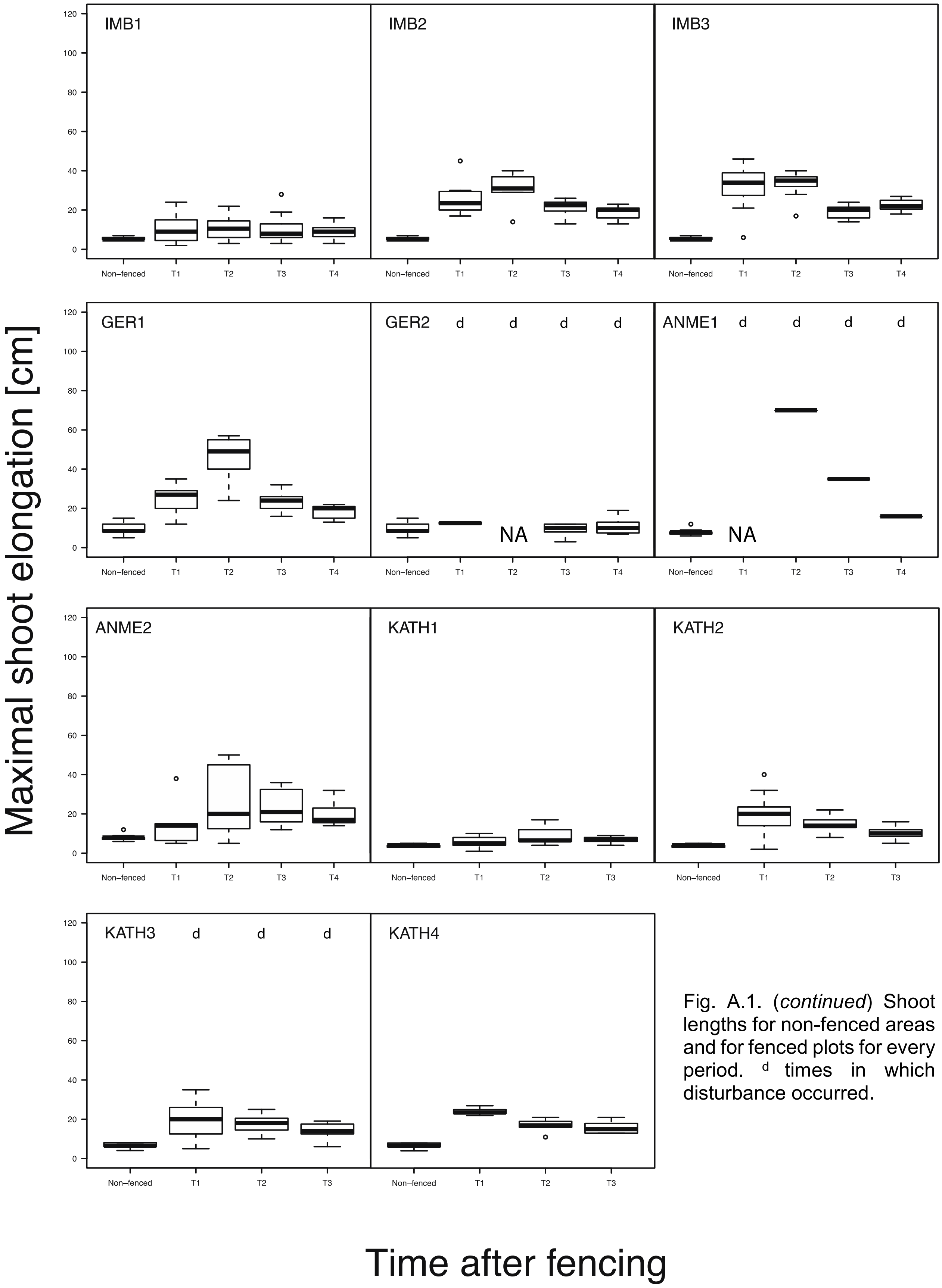

Fig. A.1. (*continued*) Shoot lengths for non-fenced areas and for fenced plots for every period. ^{d} times in which disturbance occurred.

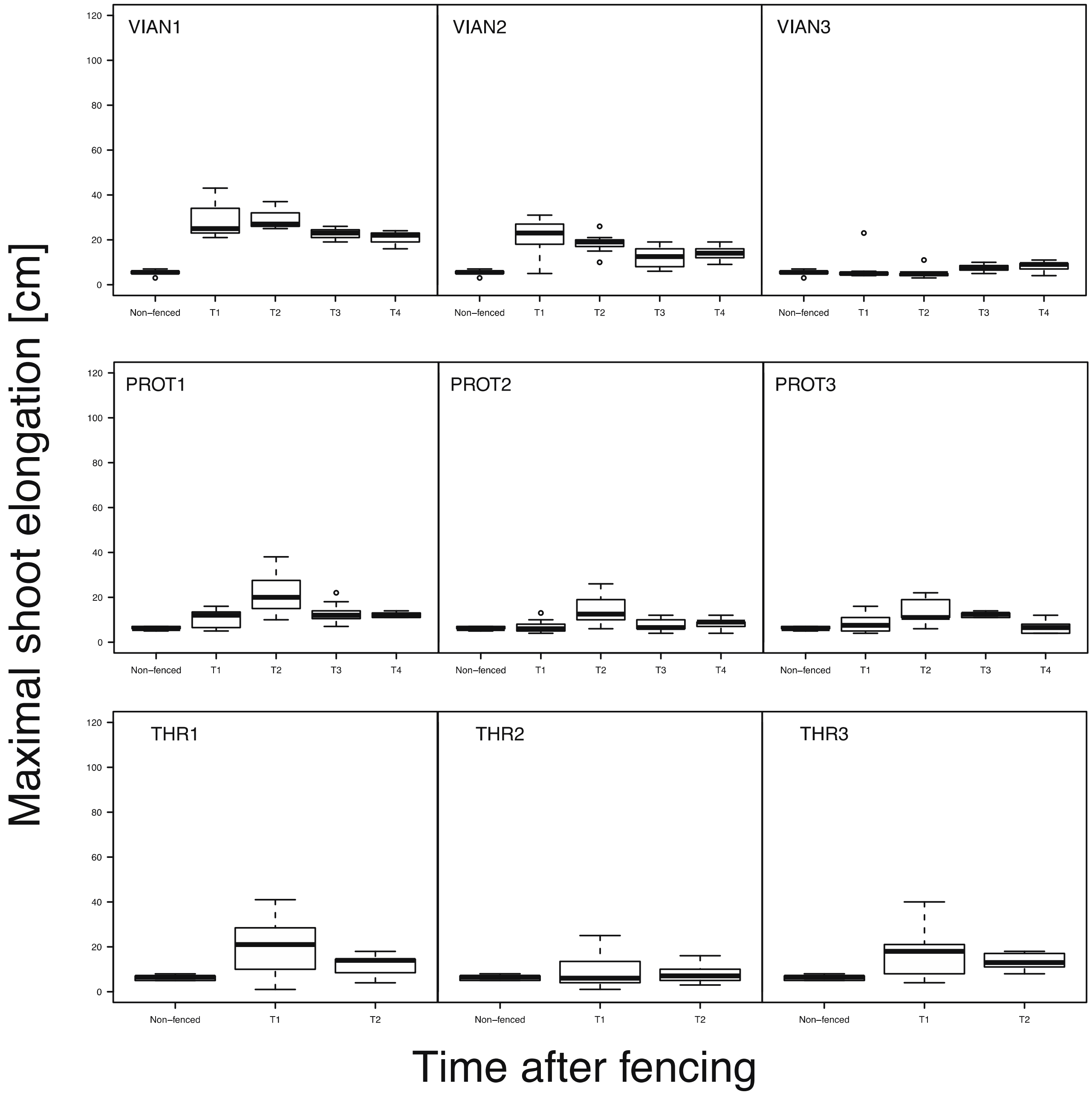

Fig. A.1. (*continued*) Shoot lengths for non-fenced areas and for fenced plots for every period. ^{d} times in which disturbance occurred.

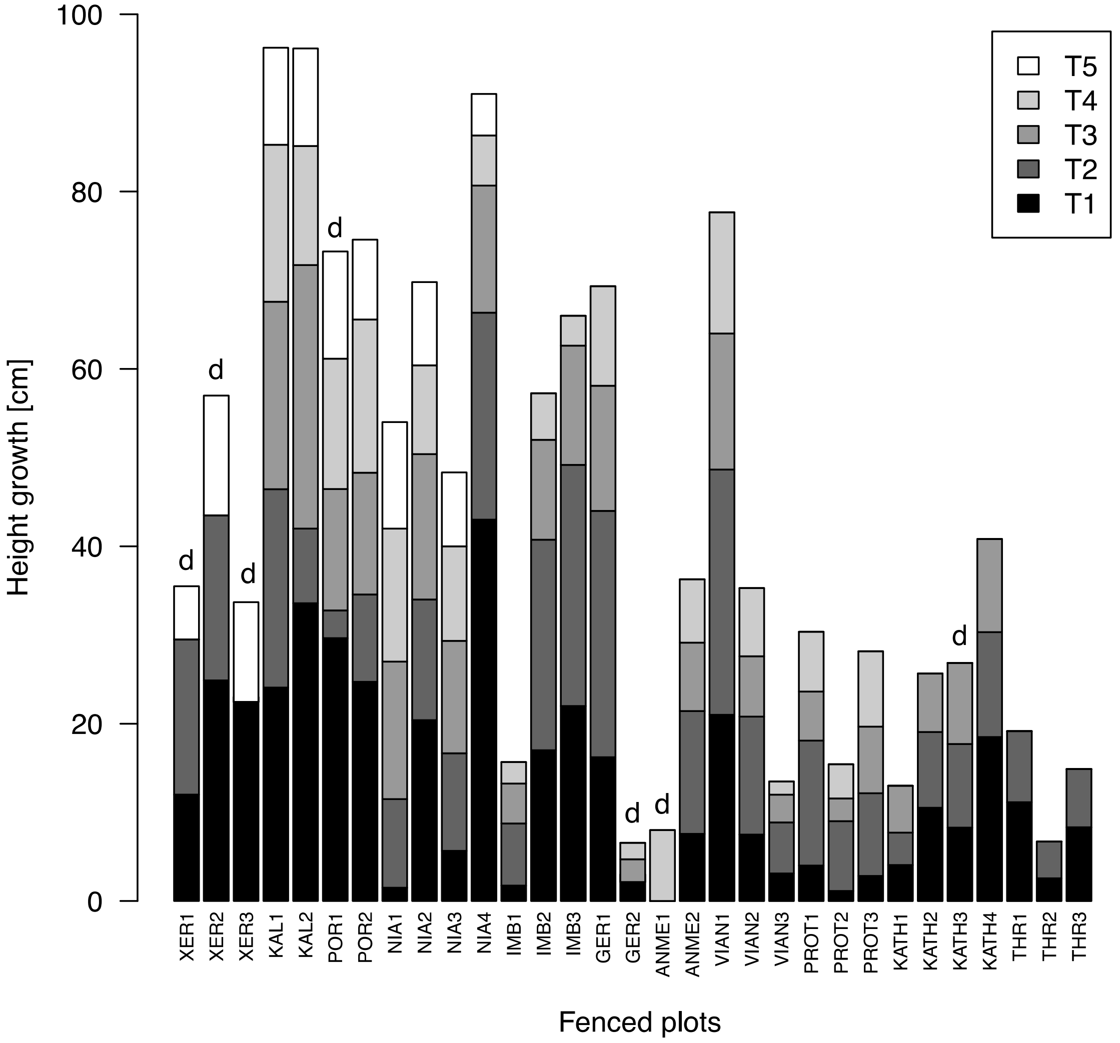

Fig. A.2. Average cumulated height growth over time (T1 to T5) for each fenced plot. ^{d} plots in which disturbance occurred.

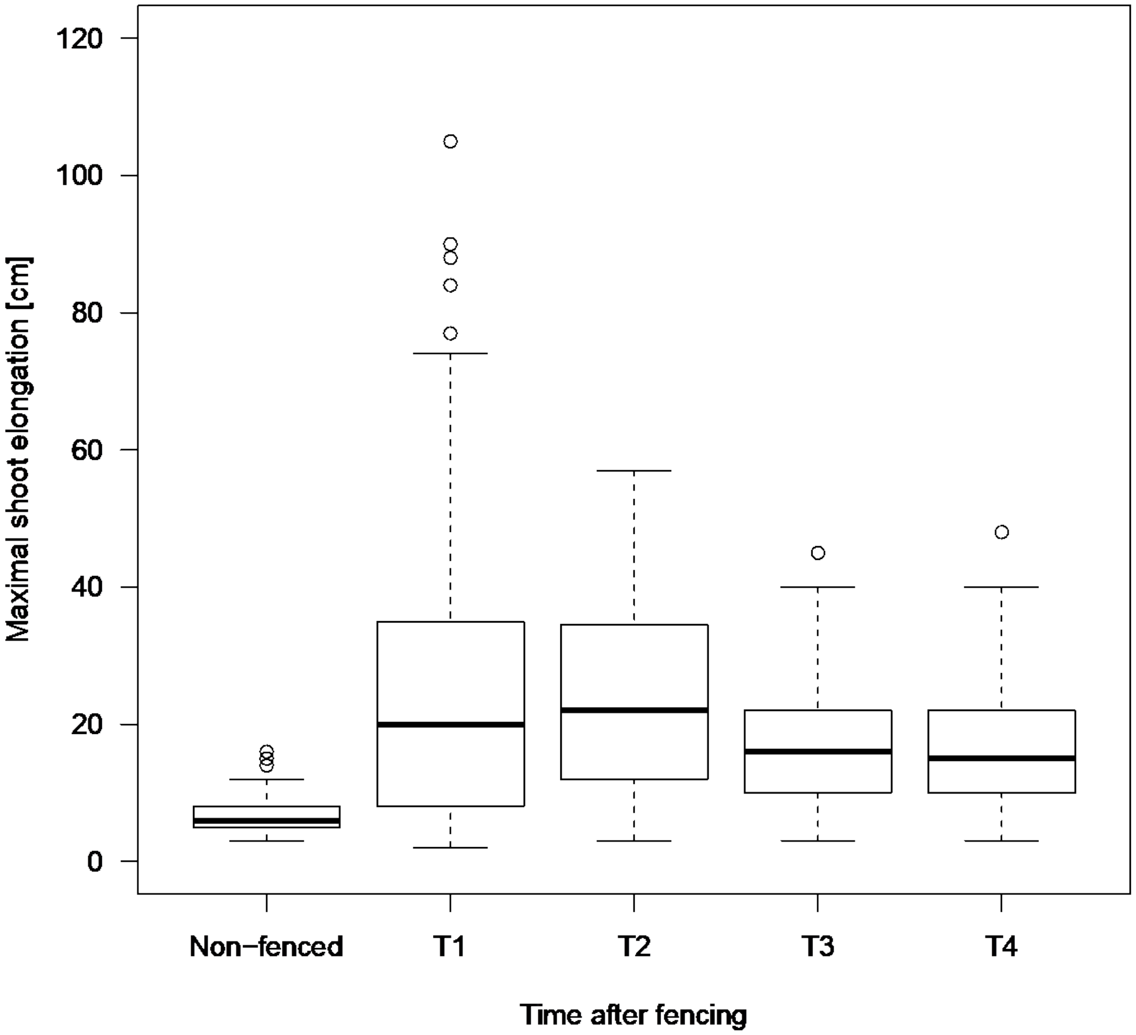

Fig. A.3. Shoot lengths of the 151 trees in 18 fenced plots for which four years of recording (T1 to T4) are available as well as 120 trees from the 12 non-fenced areas.

CHAPTER 2

UNDERSTANDING THE FACTORS INFLUENCING THE GROWTH OF *ZELKOVA ABELICEA* IN BROWSING EXCLOSURES

Laurence Fazan, Ilektra Remoundou, Dany Ghosn, Thomai Nikoli, Salvatore Pasta, Giuseppe Garfì, Gregor Kozlowski

Author contributions: LF conceived the study, DG and IR carried out field measurements, TN analyzed soil samples in the laboratory, LF performed the statistical analyses, LF wrote the manuscript, LF, SP, GG and GK reviewed the manuscript.

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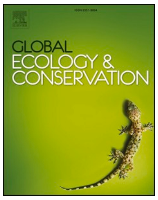

Understanding the factors influencing the growth of *Zelkova abelicea* in browsing exclosures

Laurence Fazan[a], Ilektra Remoundou[b], Dany Ghosn[b], Thomai Nikoli[c], Salvatore Pasta[d], Giuseppe Garfì[d], Gregor Kozlowski[a,e,f,*]

[a] *Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland,*
[b] *Department of Geoinformation in Environmental Management – CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100 Chania, Greece,*
[c] *Department of Sustainable Agriculture, Laboratory of Soil Science and Plant Diagnostics – CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100 Chania, Greece,*
[d] *Institute of Biosciences and BioResources – Italian National Research Council, Corso Calatafimi 414, 90129 Palermo, Italy,*
[e] *Natural History Museum Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland*
[f] *Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, 3888 Chenhua Road, Songjiang, 201602 Shanghai, China*

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ABSTRACT

The growth of *Zelkova abelicea* (Lam.) Boiss. (Ulmaceae), a tree species endemic to the island of Crete (Greece), was studied within 31 fenced plots protected from browsing during three years after fencing across the entire distribution range of the species. Potential geographic, edaphic, climatic and physiognomic factors that could influence shoot elongation and height increase were investigated for each plot. We found that trees grew twice as much within the same period of time in western and central Crete compared to trees from eastern Crete. In addition, taller trees grew more than shorter individuals. Although some variation was found within the soil parameters, and particularly sites situated on slopes were distinguishable from sites situated in flat dolines, none of the soil parameters was found to be significant in explaining growth differences amongst *Z. abelicea* trees of different mountain ranges. Precipitation and temperature were interpolated for each plot from an existing network of 49 weather stations on Crete. Our analyses showed that the plots were distributed along a longitudinal, westwards increasing gradient in precipitation as well as along an altitudinal gradient in temperature. Our analyses revealed that geographical position on the island, precipitation in June and initial tree height were significant in explaining spatial differences in *Z. abelicea* growth. Our results underline the importance of spring and early summer climatic conditions in determining *Z. abelicea* growth and highlight differences throughout the island.

1. Introduction

Tree growth is known to vary throughout the distribution range of a given species due to a number of factors. These factors may

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* Correspondence to: Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland.
E-mail addresses: laurence.fazan@unifr.ch (L. Fazan), hlektra@maich.gr (I. Remoundou), dghosn@maich.gr (D. Ghosn), thomainikoli@maich.gr (T. Nikoli), salvatore.pasta@ibbr.cnr.it (S. Pasta), giuseppe.garfi@ibbr.cnr.it (G. Garfì), gregor.kozlowski@unifr.ch (G. Kozlowski).

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include differences related to local climatic conditions, edaphic characteristics, population dynamics (e.g. tree size or age), interspecific competition or differences in herbivore pressure (e.g. Oliveira et al., 1994, Cairns and Moen, 2004, Cotillas et al., 2009, Purves, 2009, Gómez-Aparicio et al., 2011).

On the Greek island of Crete, growth of trees (and more generally of plants) is strongly controlled by (over)browsing until (if ever) they reach a sufficient height and escape herbivore pressure (Fazan et al., 2012, 2021; Zimowski et al., 2014).

Zelkova abelicea (Lam.) Boiss. (Ulmaceae), is one of three tree species endemic to Crete (Villar et al., 2015; Cambria et al., 2019; Médail et al., 2019). This Paleogene relict grows only in the Cretan mountains above 900 m a.s.l., in cool and not too xeric areas such as north-facing slopes, in or around dolines or scree slopes. However, it is also found on south-facing slopes, preferably, but not exclusively at high (>1500 m a.s.l.) altitudes. It grows oftentimes with *Acer sempervirens* L., *Quercus coccifera* L., and occasionally with *Cupressus sempervirens* L., mostly forming scattered and isolated stands (Sarlis, 1987; Egli, 1997; Søndergaard and Egli, 2006; Bauer and Bergmeier, 2011; Fazan et al., 2012; Goedecke and Bergmeier, 2018). The majority of individuals exhibit a stunted dwarfed morphology (Fig. 1A) with multiple stems and very slow growth due to severe browsing by goats (Fazan et al., 2012; Kozlowski et al., 2012). Dwarfed overbrowsed individuals do not produce fruit and can be several hundred years old, indicating almost continuous and long-lasting herbivore pressure (Sarlis, 1987; Fazan et al., 2012). Arborescent, fruiting individuals (Fig. 1B) are much rarer and represent ca. 5% of all known individuals, although proportions are very stand dependent, and most stands are dominated by dwarfed, non-fruiting individuals (Kozlowski et al., 2012). The species, irrespective of its stature, suckers abundantly and hence propagates easily vegetatively, especially when roots are exposed to mechanical damage through soil erosion and/or disturbance (Egli, 1997; Søndergaard and Egli, 2006; Fazan et al., 2012; Kozlowski et al., 2012, 2014, 2018).

Z. abelicea is listed as endangered (EN) on the IUCN Red List (Kozlowski et al., 2012). Unsustainable pastoral activities are a major threat to *Z. abelicea* (Kozlowski et al., 2012) but also more generally the most important cause of landscape degradation on Crete (Kairis et al., 2015). The presence and management of large caprine and ovine flocks prevent seedlings from establishing and dwarfed

Fig. 1. A. Dwarfed and overbrowsed *Z. abelicea* individuals, B. Arborescent fruiting *Z. abelicea* individual, C. Study plot located in the Levka Ori, D. Study plot located in the Dikti Mountains, E. Study plot located on Mt. Thripti.

individuals from growing tall and fructifying. In addition, climate variables such as seasonal precipitation quantity or temperature have been shown to be important factors for controlling growth patterns of *Z. abelicea* individuals that have reached a height sufficient to escape browsing (Fazan et al., 2017).

The impact of browsing on the growth, sexual reproduction and recruitment of *Z. abelicea* is particularly heavy in unprotected areas (Sarlis, 1987; Fazan et al., 2012, 2017, 2021). Fazan et al. (2021) showed that in the absence of browsing, *Z. abelicea* individuals grew on average twice as much as when overbrowsed. However, it remained unknown up to present if trees grew at the same rate throughout the island. Therefore, the goal of this study was to 1. evaluate the growth of *Z. abelicea* individuals in non-browsed fenced plots across the entire distribution range of the species and see if there are significant differences in growth patterns across the island, 2. characterize the fenced plots in terms of tree physiognomic, geographic, edaphic and climatic variables and identify any striking differences, 3. see if any of the above-mentioned variables can explain potential growth differences.

2. Materials and methods

2.1. Sampling procedure and collection of growth and site-specific data

Within the scope of the project for the conservation of *Z. abelicea* (www.abelitsia.gr), 31 plots (Fig. 1C-E) containing overbrowsed *Z. abelicea* individuals were fenced in twelve study areas throughout the whole distribution range of the species (Fig. 2 and see also Table 4). Plots were located in 4 of the 5 mountain ranges containing *Z. abelicea* populations: Levka Ori, Mt. Kedros, Dikti and Thripti Mountains. No plot was established on Mt. Psiloritis due to lack of arrangements with local land users in the area where the sole *Z. abelicea* population of this mountain range is found. The plots were established in order to exclude caprine and ovine browsing and trampling and to allow regrowth and fruiting of *Z. abelicea* individuals, seedling establishment and development of a non-browsed plant community. Site selection for plotting was carried out with respect to several constraints or criteria, including arrangements with local land-users, accessibility, stand structure and topography. Therefore, the morphology, including the initial height, of *Z. abelicea* individuals was variable amongst sites as some plots included well-developed, arborescent trees, i.e. out of the reach of goats (>2 m of height, see Fazan et al., 2021 for details) already at the beginning of the experiment while others contained only overbrowsed, dwarfed *Z. abelicea* individuals. Plot size was also variable, ranging from 10 to 105 m^2 due to the above-mentioned constraints and therefore the number of trees per plot also varied (see also Fazan et al., 2021 for details). Plots were not fenced all at the same time, but gradually between 2014 and 2017, and monitored annually until 2020, leading to three to six years of data collection per plot (for details see Fazan et al., 2021). In every plot, for each *Z. abelicea* individual, the length of the longest shoot produced during the year and tree height were monitored from the time the fences were installed (T0), and thereafter every year (T1, T2, etc.) at the end of the growing season in October or November. Shoot length was not measured in T0. Growth parameters were measured with a centimeter measuring stick. Since plots were established gradually and not all during the same year, growth data are available for all plots only up to T3. Therefore, for the scope of this article, the sum of shoot lengths (hereafter called shoot elongation) from T1 to T3 and the height difference (hereafter called height increase) between T0 and T3 were computed for each *Z. abelicea* individual and averaged over each plot. We found interesting to include both shoot elongation and height increase in our further analyses due to the

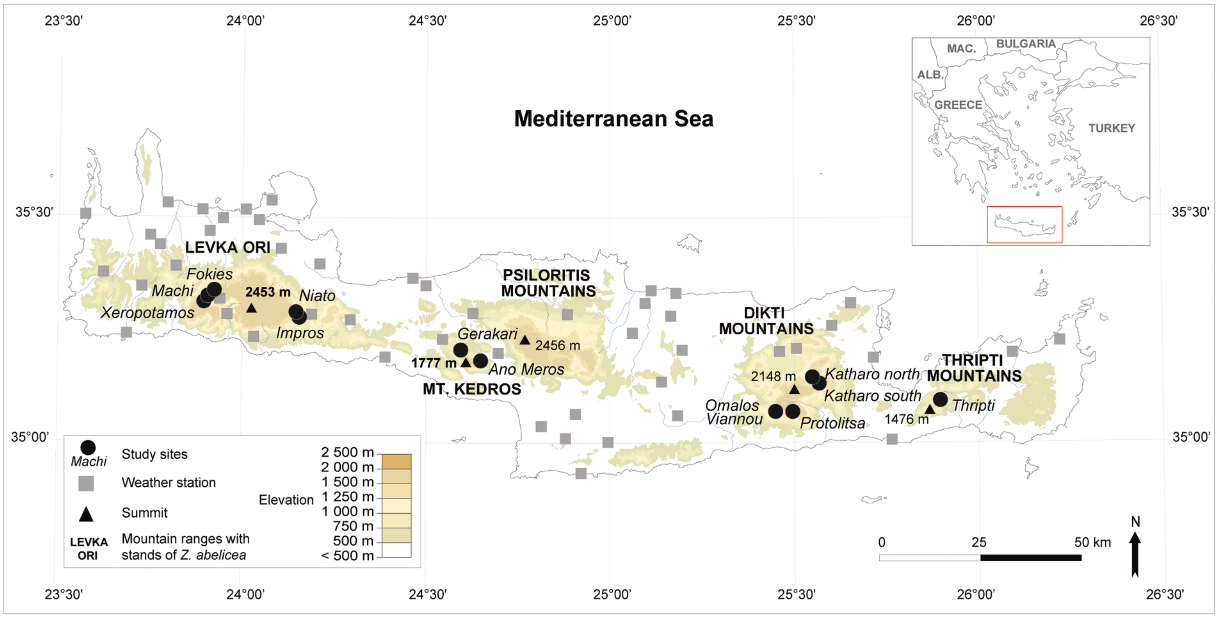

Fig. 2. Location of the 12 study sites (black circles) in which the 31 studied plots are situated, and of the 49 weather stations (grey squares) used for the weather interpolation on the island of Crete (Greece).

Table 1
Average shoot elongation between T1 and T3, height increase between T0 and T3 and average tree height at T0 for each plot. Mean average values for each mountain range are also given. Asterisks (*) indicate plots with disturbance. Mountain averages are computed only on non-disturbed plots for shoot elongation and height increase. The number of trees per plot is also given as well as the sum of trees for all plots per mountain. NA: missing or incomplete data.

Mountain	Plot	Shoot elongation (cm)	Height increase (cm)	Height at T0 (cm)	Nb of trees
Levka Ori	*XER1	85.00	NA	143.00	2
	*XER2	NA	NA	92.38	8
	*XER3	NA	NA	91.89	9
	KAL1	128.00	67.57	126.21	14
	KAL2	144.29	71.71	126.43	7
	*POR1	85.35	38.38	54.92	13
	POR2	80.29	48.29	61.57	7
	NIA1	44.77	26.00	116.33	3
	NIA2	87.20	50.40	117.60	5
	NIA3	67.83	30.75	158.25	4
	NIA4	84.33	80.67	100.67	3
	IMB1	26.87	11.26	36.81	31
	IMB2	78.38	52.00	75.63	8
	IMB3	84.27	62.64	58.91	11
	Average/sum	82.62	50.13	97.19	125
Kedros	GER1	94.11	58.11	117.67	9
	*GER2	NA	5.20	168.40	5
	*ANME1	NA	0.00	175.00	1
	ANME2	65.14	29.14	176.57	7
	Average	79.63	43.63	159.41	22
Dikti	VIAN1	70.58	56.00	147.50	4
	VIAN2	51.80	27.60	77.90	10
	VIAN3	20.26	13.30	51.30	10
	PROT1	44.64	23.64	99.18	11
	PROT2	27.95	11.13	66.20	15
	PROT3	34.17	19.67	72.50	6
	KATH1	20.43	13.00	111.36	14
	KATH2	43.58	25.29	84.79	28
	*KATH3	51.29	26.86	70.29	7
	KATH4	56.67	40.83	146.00	6
	Average	41.12	25.61	92.70	111
Thripti	THR1	44.84	26.95	63.68	19
	THR2	22.66	10.55	38.84	31
	THR3	40.80	19.72	37.68	25
	Average	36.10	19.07	46.73	75

Table 2
Results of the Wilcoxon rank sum test with continuity correction showing the significance of differences in shoot elongation (upper right panel) and height increase (lower left panel) between mountain ranges for undisturbed plots. Significant ($p < 0.05$) values are given in bold.

		Shoot elongation			
Height increase		Levka Ori	Kedros	Dikti	Thripti
	Levka Ori	–	0.35	**< 0.001**	**< 0.001**
	Kedros	0.66	–	**< 0.001**	**< 0.001**
	Dikti	**< 0.001**	**0.03**	–	0.33
	Thripti	**< 0.001**	**0.009**	0.05	–

Table 3
Results of the Wilcoxon rank sum test with continuity correction showing the significance of differences in height at T0 between mountain ranges for all plots. Significant ($p < 0.05$) values are given in bold.

	Levka Ori	Kedros	Dikti	Thripti
Levka Ori	–	**< 0.005**	0.14	**< 0.005**
Kedros	–	–	**< 0.005**	**< 0.005**
Dikti	–	–	–	**< 0.005**
Thripti	–	–	–	–

Table 4
Geographical characteristics of the fenced plots distributed in twelve localities. No aspect is given for NIA plots due to the fact that they were situated on completely flat ground. DD: decimal degrees.

Mountain	Locality	Plot	Latitude (DD)	Longitude (DD)	Altitude (m a.s.l.)	Aspect (°N)	Slope (°)	Heat load
Levka Ori	Xeropotamos	XER1	35.31	23.90	1270	25	9	2.46
		XER2	35.31	23.90	1220	35	17	2.22
		XER3	35.31	23.90	1243	35	10	2.43
	Machi	KAL1	35.32	23.92	1171	306	15	2.63
		KAL2	35.32	23.92	1195	235	22	2.96
	Fokies	POR1	35.35	23.93	1071	40	27	1.93
		POR2	35.34	23.93	1140	50	23	2.04
	Niato	NIA1	35.29	24.15	1220	–	0	2.71
		NIA2	35.29	24.15	1219	–	0	2.71
		NIA3	35.29	24.15	1211	–	0	2.71
		NIA4	35.29	24.15	1221	–	0	2.71
	Impros	IMB1	35.27	24.15	1178	85	13	2.39
		IMB2	35.27	24.15	1172	161	14	2.73
		IMB3	35.27	24.15	1178	350	5	2.62
Kedros	Gerakari	GER1	35.19	24.61	1255	190	23	2.88
		GER2	35.19	24.61	1257	358	25	2.12
	Ano Meros	ANME1	35.19	24.64	998	37	5	2.57
		ANME2	35.19	24.64	986	42	10	2.43
Dikti	Omalos Viannou	VIAN1	35.06	25.47	1324	130	10	2.62
		VIAN2	35.06	25.47	1327	135	9	2.65
		VIAN3	35.06	25.47	1309	191	6	2.79
	Protolitsa	PROT1	35.07	25.51	1637	201	37	2.90
		PROT2	35.07	25.51	1619	195	25	2.91
		PROT3	35.06	25.51	1593	237	23	2.97
	Katharo north	KATH1	35.17	25.54	1177	317	8	2.65
		KATH2	35.17	25.54	1201	252	8	2.82
	Katharo south	KATH3	35.13	25.57	1149	315	17	2.55
		KATH4	35.12	25.57	1153	344	7	2.59
Thripti	Thripti	THR1	35.08	25.89	1152	237	2	2.75
		THR2	35.08	25.89	1152	300	1	2.72
		THR3	35.08	25.89	1155	170	6	2.76

fact that growth in *Zelkova* species occurs following the Troll model (Hallé et al., 1978) with a sympodial and acrotone ramification (Garfì, 1997b) and therefore, maximum growth is not necessarily captured in height increases. In addition, initial tree height (at T0) was also averaged over each plot.

The destruction of fences through human-led or nature-induced events with subsequent browsing occurred in seven plots (XER1, XER2, XER3, POR1, GER2, ANME1, KATH3) at different times. Such plots were excluded from further analyses unless mentioned otherwise. Moreover, for some trees, measurements were missing for one or several years, either because the individual was erroneously not measured, not noticed or died at some point. Such trees were also excluded from further analyses. Therefore, a total of 288 trees with full records between T0 and T3 from 24 fenced undisturbed plots were analyzed. On average, 11 *Z. abelicea* individuals with full records were growing in the plots, but with a wide range between one and 31 trees (Table 1).

For each plot, geographical position (latitude and longitude), altitude, slope and aspect were recorded on the field. In addition, heat load, a unitless index, was computed based on latitude, slope and aspect, following the protocol described by McCune and Keon (2002) in order to get an estimation of how much heat each plot receives. Aspect was shifted by 45° so that southwest slopes have the highest heat load values and northeast slopes have the lowest heat load values (instead of southern, respectively northern oriented slopes, see McCune and Keon, 2002 for details).

2.2. Soil data

Surface soil samples were collected from the upper 35 cm of soil in each of the 31 fenced plots, in spring 2019. The samples were air-dried, ground to pass a 2 mm sieve and analyzed for selected physical and chemical properties. Soil particle size was analyzed following the methods described by Bouyoucos (1962). The relative proportion (%) of sand, silt and clay was used to classify samples into one of 12 soil texture classes following the USDA classification (Soil Science Division Staff, 2017 and see Fig. S3 for more details). PH was measured in a soil/water suspension at a 1:2 ratio, the proportion of organic matter was determined with the wet oxidation method (Walkley and Black, 1934), and electrical conductivity as measured in the saturation paste extract (Rhoades, 1996).

For the available forms of nutrients, nitrate nitrogen NO_3-N was extracted with 1 M potassium chloride. Phosphorus (P) was extracted by 0.5 M sodium bicarbonate (pH 8.5). Phosphorus was then quantitatively determined following the molybdenum blue-ascorbic acid method (Olsen and Sommers, 1982) and determined with Vis-UV spectrophotometry. Exchangeable cations potassium (K) and magnesium (Mg) were extracted with 1 M ammonium acetate (pH 7) (Thomas, 1982) and analyzed by the inductively coupled plasma method (ICP-OES). For trace element determination, the four metals: iron (Fe), copper (Cu), zinc (Zn) and manganese (Mn) were extracted with the DTPA method developed by Lindsay and Norvell (1978) and boron (B) was extracted with the hot water method (Keren, 1996). The soil texture diagram was done in R (version 4.0.2, R Core Team, 2021) with the package soiltexture (Moeys, 2018).

2.3. Interpolated weather data

Weather data (i.e. minimum, maximum and mean daily temperature and total daily precipitation) from October 2014 to September 2020 were uploaded from the 49 Cretan weather stations that had available data for that period, provided by the Environmental Research Institute of the National Observatory of Athens (Lagouvardos et al., 2017) and available online (meteosearch.meteo.gr; and see also Table S1 and Fig. 2). Some stations showed incomplete or missing data for some hours or days and for some variables. In all cases, incomplete or missing values were replaced by "NA" for the full concerned time period. In order to have an estimation of temperature and precipitation at the fenced plots, interpolation was carried out in R using package meteoland (De Cáceres et al., 2018; De Cáceres and Granda, 2021). This package allowed interpolation of the daily station weather data based on the latitudinal, longitudinal and altitudinal position of sites, by taking into account minimum and maximum temperature and precipitation records from nearby known weather stations. The following variables were interpolated: daily mean, maximum and minimum temperature and precipitation sum. Prior to interpolation, optimal parameters α (Gaussian shape parameter) and N (number of stations) were determined for minimum and maximum temperature, precipitation occurrence and precipitation amount (see De Cáceres et al., 2018 and De Cáceres and Granda, 2021 for details). For minimum and maximum temperature, optimal α was 0.5 and N was 49. For precipitation occurrence optimal α was 2.5 and N was 3. For precipitation amount, optimal α was 0.5 and N was 49, showing that all available stations needed to be included in the model in order to best predict precipitation amounts. However, considering the importance of local topographical features, the scarcity of weather stations in some areas and the presumable existence of a longitudinal gradient in precipitation (see e.g. Agou et al., 2019; Goedecke and Bergmeier, 2018; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012), we decided to define N as 10. This way, only the 10 closest weather stations are used to estimate precipitation amounts in a given site (for the sake of comparison, cross validation statistics for the original optimal $N = 49$ can be found in Table S2). Evaluation of the prediction errors for all meteorological variables was carried out by leave-one-out cross validation. The performance of each variable was assessed using mean absolute error (MAE), bias and Pearson's correlation coefficient (De Cáceres et al., 2018; De Cáceres and Granda, 2021). Interpolations were carried out for each of the 31 fenced plots over the above-mentioned period. The interpolated daily data was then averaged first monthly for mean, minimum and maximum temperature and then annually, or for precipitation first summed monthly and then annually for each fenced plot. Once monthly (for precipitation) or annual (for both precipitation and temperature variables) data were obtained, they were averaged once again over the full period from October 2014 to September 2020, in order to get a single monthly or annual value for every variable.

2.4. Statistical analyses

All statistical analyses were carried out in R. Kruskal-Wallis rank sum tests (kruskal.test, Hollander and Wolfe, 1973) were carried out on the 24 non-disturbed fenced plots in order to look for statistically significant differences in total shoot elongation, total height increase as well as tree height at T0 amongst plots. Pairwise Wilcoxon rank sum tests with continuity correction (pairwise.wilcox.test, package stats, R Core Team, 2021) were carried out on non-disturbed fenced plots to check for and assess significant differences in shoot elongation and height increase, and on all plots to assess significant differences in height at T0 among mountain ranges. In addition, correlations between *Z. abelicea* shoot elongation, height increase and initial tree height were computed with Spearman's rho (cor.test, package stats, R Core Team, 2021) correlation coefficient.

Principal component analysis (Borcard et al., 2011) was carried out using function rda from package vegan (Oksanen et al., 2019) on the 24 non-disturbed fenced plots separately for the geographic variables (longitude, latitude, altitude, slope, heat load), soil variables (pH, organic matter, electrical conductivity, NO_3-N, P, K, Mg, Fe, Mn, Zn, Cu and B) and interpolated weather data (16 variables: interpolated averaged minimum, mean and maximum annual temperature, averaged sum of annual precipitation and monthly previous October to current September averaged total precipitation) in order to investigate and visualize the different variables and main trends in the data.

In order to see which variables could possibly explain the spatial variation in *Z. abelicea* growth, redundancy analysis (Borcard et al., 2011) was carried out on the 24 non-disturbed fenced plots using function rda from package vegan (Oksanen et al., 2019). Response variables were *Z. abelicea* height increase from T0-T3 and shoot elongation from T1-T3. The variables included in the geographic, soil and interpolated weather datasets described above for principal component analysis were here included as three separate explanatory datasets. In addition, average tree height at T0 was included as a fourth dataset to represent tree physiognomy.

Due to the high number of variables and the occurrence of several separate datasets (i.e. geographic variables, interpolated climatic variables, soil variables and initial tree height), four separate redundancy analyses were carried out on each of the datasets in order to check for significance of each dataset and remove highly collinear variables within a dataset and reduce variable number.

Prior to analysis, response and explanatory variables were standardized to zero mean and unit variance using function decostand (package vegan, Oksanen et al., 2019). Permutation tests were carried out (anova.cca, package vegan, Oksanen et al., 2019) to test the significance ($p < 0.05$) of each of the four redundancy analysis results as well as the canonical axes, with 1000 permutations. Linear dependencies amongst explanatory variables were checked through variance inflation factors (VIFs, vif.cca, package vegan, Oksanen et al., 2019). For datasets that had variables with VIFs above 10, forward selection was performed (forward.sel, package adespatial, Dray et al., 2020). The adjusted R^2 (RsquareAdj, package vegan, Oksanen et al., 2019) of the model containing all potential variables of the dataset was used as a stopping criterion. Through these analyses, a reduced number of variables within the four datasets were found to be significant and were included in the final redundancy analysis. This time, we computed a partial redundancy analysis (Borcard et al., 2011) where *Z. abelicea* growth is explained by the final selected climatic, geographic or soil variables, while at the same time holding initial tree height constant due to its known correlation with tree growth. The adjusted R^2 of the final redundancy analysis, as well as of each dataset alone or in relationship with one another were computed (varpart, package vegan, Oksanen et al., 2019, Borcard et al., 2011) in order to express the explained variance. Significance of the final model was tested again through permutations.

3. Results

3.1. Spatial growth differences

Total shoot elongation and total height increase for each fenced plot, as well as for every mountain are found in Fig. 3 and Table 1. On average, trees in the Levka Ori and Kedros grew two times more than trees from Dikti and Thripti. The Kruskal-Wallis rank sum test showed that significant differences in shoot elongation or height increase do exist (respectively $X^2=202.31$, df=23, $p < 0.001$; $X^2=183.8$, df=23, $p < 0.001$) between fenced plots. The pairwise Wilcoxon rank sum test showed in addition that trees from Levka Ori and Kedros have significantly ($p < 0.05$) higher growth (both for shoot elongation and height increase) than trees from Dikti or Thripti (Table 2). Trees from Levka Ori and Kedros showed similar growth in relation to each other, while trees from Dikti and Thripti also showed similar growth in relation to one another.

Tree height at T0 was also found to be significantly different between plots ($X^2=139.63$, df=23, $p < 0.005$), as well as between mountain ranges (Fig. 4 and Table 3). Trees sampled within the fenced plots on Mt. Kedros were significantly higher at T0 than trees in the three other mountain ranges. Trees in the Levka Ori and Dikti Mountains had a similar height at T0, while trees in the Thripti Mountains were significantly smaller than elsewhere. Furthermore, a positive correlation exists between tree height at T0 and shoot elongation (rho=0.50, $p < 0.001$) as well as for height increase (rho=0.41, $p < 0.001$), indicating that taller trees tend to have a higher growth rate than dwarfed trees, as was already previously pointed out by Fazan et al. (2021).

3.2. Geographical characteristics of plots

Geographical variables for each plot are reported in Table 4. The principal component analysis (Fig. S1) shows that the majority of

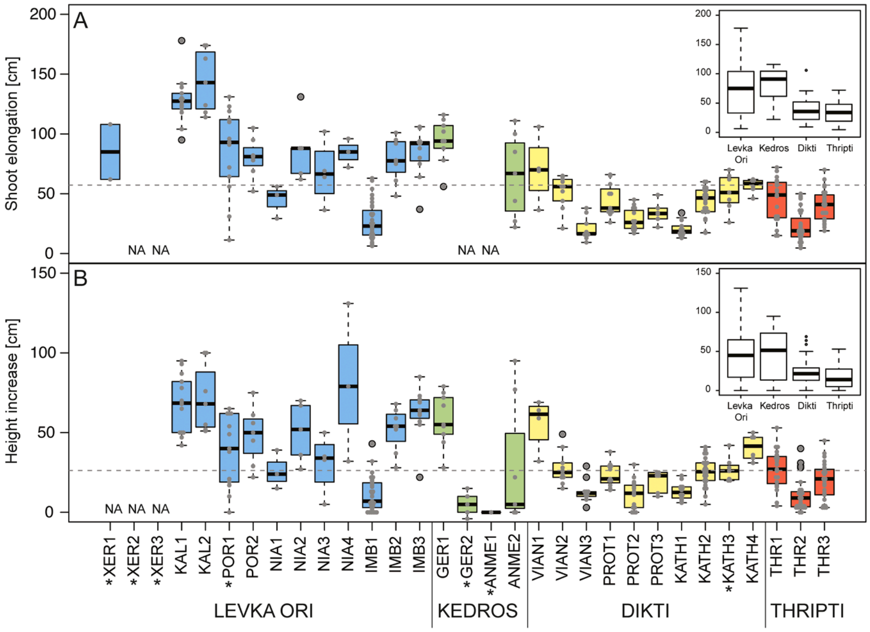

Fig. 3. A. Total shoot elongation from T1 to T3, B. Total height increase from T0 to T3, for each fenced plot. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as open circles. Individual trees per plot are represented by grey dots. The overall median (of undisturbed plots) is expressed by the grey dotted line. * indicate plots with disturbance. The miniatures show boxplots for each mountain range. Plots and mountains are ordered according to their geographical position, going from west to east. Colors show different mountains (blue: Levka Ori, green: Mt. Kedros, yellow: Dikti, red: Thripti).

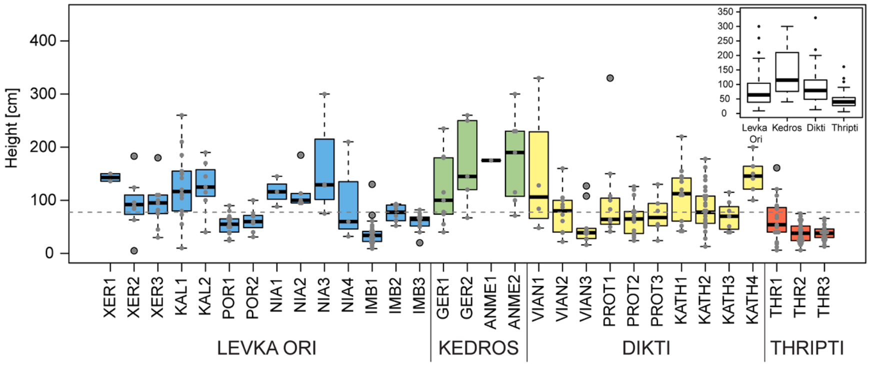

Fig. 4. Initial tree height at the time the fences were established (T0) for each fenced plot. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as open circles. Individual trees per plot are represented by grey dots. The overall median of all plots is represented by the grey dotted line. The miniatures show boxplots for each mountain range. Plots and mountains are ordered according to their geographical position, going from west to east. Colors show different mountains (blue: Levka Ori, green: Mt. Kedros, yellow: Dikti, red: Thripti).

plots is clustered together but clearly organized following their geographical (latitude and longitude) position on the island. The first two axes explain 79% (52% and 27%, respectively) of the variance. Eastern sites are also situated more to the south compared to western plots. In addition, heat load is strongly linked with geographical position, with trees in eastern Crete having a higher heat load index compared to those in western Crete. Protolitsa plots (PROT1, PROT2, PROT3) stand out by their higher than elsewhere altitude.

3.3. Soil characteristics of plots

Soil variables for each plot are found in Table 5. The principal component analysis (Fig. S2) shows that most plots are clustered together and therefore show similarities for most of the pedological variables (Fig. S2A). The first two axes explain 54% (36% and 18%, respectively) of the variance. However, plots from Niato (NIA1, NIA2, NIA3, NIA4) and Thripti (THR1, THR2, THR3) stand out by their higher nutrient content, higher percentage of organic matter, higher electrical conductivity and lower pH than most other sites. Plots from Machi (KAL1, KAL2) and Xeropotamos (XER1, XER2, XER3) have higher P and Zn. Generally speaking, most (but not all) plots in western Crete have higher organic matter content than plots further east (with the exception of Thripti). Soil texture (Table 5 and Fig. S3) varied amongst plots, while some plots in the Levka Ori had a higher silt content than elsewhere, and some plots in Dikti had higher sand content than elsewhere. In addition, plots from Thripti were more homogenous with regards to their clay content compared to the other mountain ranges. The soils within the plots were classified as clay, clay loams, loams, sandy clay loams and sandy loams.

3.4. Weather variability

The performance of each interpolated variable is reported in Table 6. Mean absolute errors for predicted versus observed values were of 2.23 °C for daily minimum temperature and 1.64 °C for maximum temperature, with high correlation coefficients. Bias for minimum temperature was − 0.02 °C and for maximum temperature 0.01 °C. The prediction of temperature ranges resulted in a MAE of 2.25 °C, a correlation coefficient of 0.57 and a bias of 0.03 °C. MAE for annual station rainfall was 1405.93 mm, with a correlation coefficient of 0.66 and a bias of 97.83 mm. The principal component analysis (Fig. S4) showed a clear distinction between plots. The first axis mainly explains precipitation patterns, where plots from western Crete (Levka Ori) and Kedros stand out by their higher than elsewhere precipitation levels for most months, as well as for annual precipitation. Plots from Dikti show intermediate values, while plots from Thripti have lower than elsewhere precipitation. There is a difference between plots from the eastern and western Levka Ori. The eastern Levka Ori plots (Niato and Impros) show higher precipitation levels for all months than the western Levka Ori (Xeropotamos, Machi and Fokies) plots. The latter are more similar to what occurs on Mt. Kedros. In addition, plots from the western Levka Ori seem to have less abundant precipitation values for several months (i.e. October and December of the previous year and April and May of the current year), a pattern which is not visible in the eastern Levka Ori plots. The second axis represents mainly temperature gradients, with the high altitude Protolitsa plots (Mt. Dikti) showing lower than elsewhere temperature and a clear distinction between plots of Mt. Kedros, with the lower lying Ano Meros plots showing higher temperatures than the plots of Gerakari. Plots from eastern Crete seem to have overall lower annual temperatures than those of western Crete. The first two axes explain altogether 92% of the variance (62% and 30%, respectively).

3.5. Relationships between growth and explanatory variables

From the four initial datasets (geographic, physiognomic, soil and interpolated weather), the combined use of permutation tests and forward selection revealed that only longitude, precipitation in June and initial tree height were significant (Fig. 5), and only the

Table 5
Soil characteristics of each fenced plot. Org. mat: organic matter, Text. class: textural class, El. cond: electrical conductivity.

Plot	pH	Org. mat (%)	Texture (%)			Text. class	El. cond (mS/cm)	Nutrients (mg/kg)								
			Sand	Silt	Clay			NO_3-N	P	K	Mg	Fe	Mn	Zn	Cu	B
XER1	7.90	6.50	45.30	44.00	10.70	loam	0.24	2.50	25.00	71.00	64.00	18.50	14.40	8.10	1.10	0.97
XER2	8.30	4.70	61.30	30.00	8.70	sandy loam	0.22	3.60	17.00	65.00	53.00	12.60	9.50	2.90	0.74	0.65
XER3	7.50	4.60	45.30	42.00	12.70	loam	0.41	5.50	12.00	79.00	73.00	16.80	19.10	2.00	0.86	0.70
KAL1	7.80	6.80	38.60	50.00	11.40	silt loam	0.28	4.80	7.00	77.00	88.40	21.80	32.10	5.40	1.40	0.77
KAL2	7.60	11.30	38.60	48.00	13.40	loam	0.18	5.00	9.00	123.00	153.00	17.80	21.40	2.10	2.10	0.91
POR1	7.60	2.30	10.60	32.00	57.40	clay	0.12	0.70	4.00	186.00	190.00	11.60	10.40	0.30	1.20	1.30
POR2	7.50	1.30	10.60	26.00	63.40	clay	0.13	1.10	4.00	165.00	404.00	9.50	12.70	0.38	1.10	0.61
NIA1	7.40	9.40	32.60	32.00	35.40	clay loam	0.12	2.60	7.00	212.00	990.00	21.70	30.20	3.60	1.80	1.00
NIA2	6.10	9.40	32.60	26.00	41.40	clay	0.36	24.00	7.00	264.00	427.00	30.90	58.90	2.20	1.80	0.94
NIA3	6.90	8.40	26.60	28.00	45.40	clay	0.70	4.80	6.00	374.00	807.00	31.90	43.80	2.80	1.90	0.60
NIA4	7.20	6.40	28.60	28.00	43.40	clay	0.48	3.10	5.00	161.00	810.00	25.00	21.90	2.00	2.00	0.74
IMB1	7.30	6.20	22.60	36.00	41.40	clay	0.21	3.40	5.00	194.00	143.00	15.80	54.40	1.30	2.30	0.69
IMB2	7.80	5.30	28.60	44.00	27.40	clay loam	0.26	10.10	6.00	155.00	90.40	13.40	26.30	2.10	1.50	0.87
IMB3	6.90	4.50	42.60	26.00	31.40	clay loam	0.12	12.00	5.00	126.00	102.00	15.60	42.90	0.63	1.00	0.68
ANME1	7.80	2.90	54.60	24.00	21.40	sandy clay loam	0.15	3.80	6.00	111.00	98.40	16.90	27.50	0.69	1.90	0.66
ANME2	8.10	3.10	34.60	30.00	35.40	clay loam	0.16	0.50	13.00	111.00	110.00	18.20	26.30	0.90	3.00	0.56
GER1	7.70	4.70	22.60	30.00	47.40	clay	0.24	5.60	8.00	269.00	224.00	21.00	50.60	1.40	4.00	0.79
GER2	7.90	1.30	4.60	36.00	59.40	clay	0.17	0.50	5.00	441.00	204.00	15.30	30.80	0.54	1.90	0.70
VIAN1	7.70	2.20	43.30	23.00	33.70	clay loam	0.23	3.50	4.00	154.00	98.70	11.90	17.10	0.75	2.60	0.47
VIAN2	7.90	4.40	37.30	26.00	36.70	clay loam	0.23	4.20	6.00	229.00	98.80	16.40	28.70	1.10	2.40	0.58
VIAN3	8.00	2.40	57.30	20.00	22.70	sandy clay loam	0.21	3.70	4.00	117.00	110.00	11.70	15.90	0.58	1.20	0.45
PROT1	7.90	6.40	47.30	28.00	24.70	sandy clay loam	0.30	9.40	9.00	226.00	158.00	12.90	14.90	0.74	1.20	0.69
PROT2	7.60	4.30	37.30	28.00	34.70	clay loam	0.17	6.70	6.00	176.00	202.00	15.40	24.90	0.89	2.50	0.72
PROT3	7.60	3.80	23.30	32.00	44.70	clay	0.19	6.80	5.00	309.00	309.00	13.10	25.30	0.58	2.60	0.79
KATH1	7.60	1.90	13.30	22.00	64.70	clay	0.15	3.70	4.00	150.00	303.00	8.00	12.40	0.31	0.50	0.58
KATH2	7.30	2.80	19.30	24.00	56.70	clay	0.10	2.50	4.00	197.00	316.00	10.40	27.10	0.62	0.66	0.60
KATH3	7.90	1.40	71.30	16.00	12.70	sandy loam	0.12	3.50	5.00	46.70	128.00	13.80	4.50	0.17	1.50	0.46
KATH4	7.70	2.10	65.30	18.00	16.70	sandy loam	0.18	1.70	3.00	74.80	119.00	19.00	6.10	0.30	1.20	0.52
THR1	6.50	5.70	18.60	28.00	53.40	clay	0.13	5.70	8.00	401.00	526.00	26.00	54.40	2.60	2.00	1.10
THR2	7.40	6.70	32.60	22.00	45.40	clay	0.25	3.70	7.00	544.00	968.00	11.60	39.40	4.50	1.30	1.50
THR3	7.20	3.90	18.60	30.00	51.40	clay	0.15	0.50	10.00	313.00	571.00	15.90	40.00	1.70	2.20	0.92

Table 6
Leave-one-out cross validation statistics for the interpolation procedure for the 49 weather stations with available data for the period October 2014 to September 2020. n: number of stations or number of days, r: linear correlation coefficient, MAE: mean absolute error. SD stations: standard deviation of MAE across stations, SD days: standard deviation of MAE across days. Date rainfall: sum of precipitation across stations for each date. Date precipitation stations: number of stations with precipitation events for each date.

Variable	n	r	MAE			Bias		
			Value	SD stations	SD days	Value	SD stations	SD days
Minimum temperature (°C)	84991	0.90	2.23	0.97	0.42	-0.02	2.28	0.07
Maximum temperature (°C)	84972	0.95	1.64	0.83	0.32	0.01	1.56	0.06
Temperature range (°C)	84969	0.57	2.25	1.06	0.67	0.03	2.21	0.09
Station annual rainfall (mm·yr^{-1})	49	0.67	1359.23	1304.88	NA	-4.62	1894.38	NA
Station precipitation days	49	0.47	92.00	80.91	NA	-9.39	122.78	NA
Date rainfall (mm)	1429	0.99	9.44	NA	22.89	-0.12	NA	24.76
Date precipitation stations	1429	0.99	1.15	NA	1.26	-0.21	NA	1.69

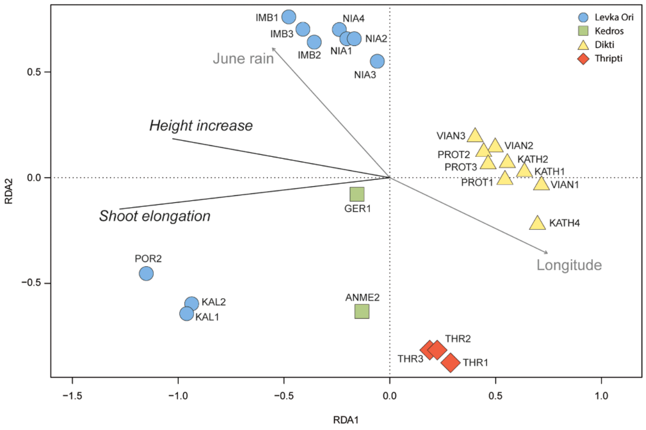

Fig. 5. Partial redundancy analysis correlation triplot of tree growth (shoot elongation and height increase) in the 24 non-disturbed *Z. abelicea* fenced plots explained by geographic (longitude) and climatic (June rain) variables when considering initial tree height as constant. Projecting a plot at right angle on a variable approximates the value of the plot along that variable. Distances amongst plots are not approximations of their Euclidean distance. Plots are distinguished by mountain range through different colors and symbols (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti). Scaling 2 was applied which means that projecting a plot at right angle on a response or explanatory variable approximates the value of the plot along the variable. The angles between response and explanatory variables and between response variables themselves or explanatory variables themselves reflect their correlations (Borcard et al., 2011).

first constrained axis was significant (Table S3). None of the soil variables was found to be significant in the initial redundancy analysis and therefore none were kept for further analyses. The final redundancy analysis explained 52% (adjusted R^2) of the variation in *Z. abelicea* growth. Longitude alone explained 22%, June rain explained 7%, while initial tree height explained 5% (Fig. 6).

4. Discussion

4.1. Size, habit and growth patterns

When protected from browsing, *Z. abelicea* trees were found by Fazan et al. (2021) to grow on average twice as much as their overbrowsed counterparts. Here we revealed in addition a clear difference in both shoot elongation and height increase according to the location of the trees. Both shoot elongation and height increase of protected from browsing *Z. abelicea* individuals from western (Lekva Ori) and central (Mt. Kedros) mountains of Crete was significantly higher, on average two times more, than their eastern (Dikti and Thripti) counterparts.

Our analyses revealed that initial tree height was strongly and significantly positively correlated with both shoot elongation and height increase, as was already shown by Fazan et al. (2021), and that some differences occurred between mountain ranges, with Kedros having significantly taller trees than elsewhere and Thripti having significantly smaller trees. Some of these height variations are most probably related to the sampling procedure (i.e. which trees were fenced), but also to differences in population structure (Kozlowski et al., 2014). Indeed, *Z. abelicea* population structure shows differences amongst sites, with some sites, such as Thripti composed only of dwarfed overbrowsed individuals, whereas other sites have both dwarfed and normal growing trees, in varying proportions (Kozlowski et al., 2014).

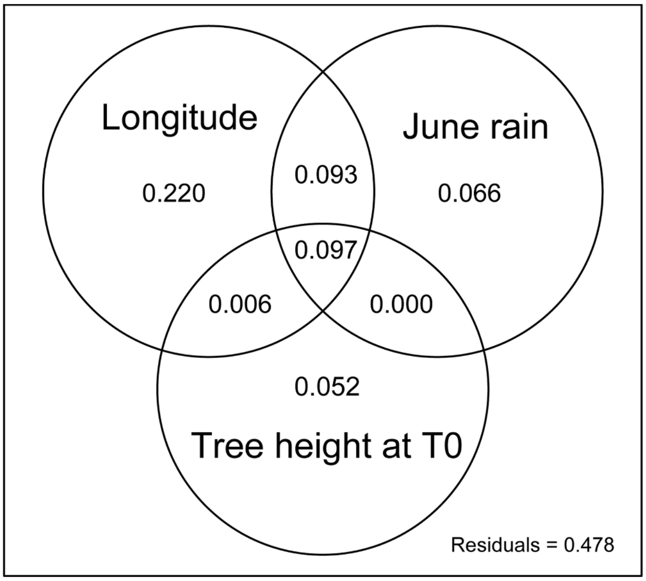

Fig. 6. Variation partitioning of the three different explanatory datasets (physiognomic, geographic and climatic), each containing in our case only one variable (Tree height at T0, longitude and precipitation in June) that were included in the final redundancy analysis. Values represent the adjusted R^2 for each part. The total amount of variation in *Z. abelicea* growth explained by the model is 52%. The intersection between circles shows the part of variation that is explained conjointly by two or more datasets.

4.2. The role of geography

Plots containing *Z. abelicea* trees are distributed along a longitudinal as well as latitudinal gradient, due to the geographical position of Crete and its mountains (Fig. 2 and Fig. S1). Therefore, plots in western Crete are situated more to the northwest, those in central Crete are intermediate and those in eastern Crete have a more southeast position. Heat load was found to be higher in the eastern plots compared to the western plots. This could be linked with the fact that eastern plots are located at a slightly lower latitude than western plots. However, the latitudinal difference between the northernmost and southernmost plot is very small and amounts only to 0.29'. Therefore, our finding is most probably linked to the fact that the majority of the investigated plots in eastern Crete have a more southerly aspect than western plots, which means higher heat load values. The three Protolitsa and the three Omalos Viannou plots are indeed located on south facing slopes. However, it cannot be generalized that *Z. abelicea* trees in eastern Crete grow in majority on south-facing slopes since this feature relies strongly on the sampling procedure. To our knowledge, trees situated on north-facing slopes also occur in eastern Crete but were coincidently only rarely sampled in this study. Indeed, Goedecke and Bergmeier (2018), who analysed more records of *Z. abelicea* than those included in the present study, did not find any differences between western and eastern Crete for heat load. In any case, the differences found for heat load in the present article were not significant in explaining growth differences between western and eastern *Z. abelicea* plots.

4.3. Soil properties

In this study, we provide information about soil physical and chemical properties and soil nutrient content throughout the range of *Z. abelicea* (with the exception of the population on Mt. Psiloritis) for the first time. Egli (1993) had previously studied in depth the soil characteristics of dolines of Crete, some of which hosted *Z. abelicea* trees, but he did not analyse the nutrient content of soil samples, nor did he consider the *Z. abelicea* sites located on slopes. In our study, soil parameters did not show any striking differences in terms of chemical composition or texture amongst plots. Indeed, most of the plots are clustered in Fig. S2A, showing relatively similar features. However, we did find that plots of Thripti and Niato tend to have a higher nutrient content, higher organic matter content, higher electrical conductivity and lower pH than other plots. These plots have the particularity of being the only sampled plots that are situated in flat karstic poljes or dolines floors (for a precise definition of terms dealing with karstic landscapes, see Egli 1993), at the foot of slopes. All other plots are situated on more or less steep, sometimes terraced, slopes. Dolines are known to receive more nutrients and be moister than slopes (Bátori et al., 2017), through the accumulation of eroded material and runoff. Similarly to what we found in our study, Filibeck et al. (2019) found a positive correlation between slope and pH, with doline bottoms and the foot of slopes having lower pH values than slopes. Steep slopes often have thin soils, little soil accumulation and have surfacing or outcropping limestone, which has a higher pH value (Filibeck et al., 2019). Dolines on Crete are known to have deeper soils with a higher proportion of organic matter compared to adjacent sloped areas (Vogiatzakis et al., 2003). More generally speaking, doline soil in the Mediterranean is often more acidic than slopes, through the accumulation of clay rich, decarbonated soil and wind-blown siliceous material (e.g. Saharan dust) (Filibeck et al., 2019). In addition, plots from the Levka Ori showed slightly higher organic content than plots elsewhere, and the plots from Omalos show higher P and Zn content. Several sites from western Crete seem to have higher silt content than elsewhere, whereas those of Thripti are more homogeneous in terms of clay content. These trends could be linked to differences in the parent material, bedrock, land use or sample selection. However, none of the soil parameters was found to be significant in explaining growth differences amongst *Z. abelicea* trees and further investigations should be undertaken to investigate more these points.

4.4. Weather data variability and climatic patterns

The interpolated weather data allowed a clear distinction between plots according to the rainfall and temperature patterns of nearby weather stations. The model gives a rather precise estimation of temperature. However, results are less precise when it comes to estimating precipitation quantities, and the model gave larger errors. This is most probably imputable to several factors. Firstly, Crete possesses a highly complex topography, which strongly modulates precipitation regimes and places that will receive or not rain. Rainfall is known to be highly variable according to orographic factors, continentality (i.e. distance from the coastline), direction of prevailing winds, topography and aspect (Naoum and Tsanis, 2003). Secondly, the network of weather stations used in this study is rather scanty in some areas (e.g. eastern Crete) and absent from the mountainous areas between 900 and 1800 m a.s.l. where *Z. abelicea* grows. Indeed, only one station is located above 900 m a.s.l., while the median altitude of weather stations used in this study currently lies at 170 m a.s.l. Finally, the model used for interpolation of temperature and precipitation data allows for a correction for altitude only (De Cáceres and Granda, 2021). This explains why plots from Protolitsa (higher altitude than all other plots) stand out (Fig. S4). Indeed, precipitation is known from Crete, and more generally, to increase with rising altitude (e.g. Agou et al., 2019; Naoum and Tsanis, 2003; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012). However, differences in precipitation from windward, north-facing slopes versus leeward, south-facing slopes of Crete have been previously described (Naoum and Tsanis, 2003). Unfortunately, the model used in our study is not complex enough to also include corrections for topography or lee-side effects.

A west to east decreasing precipitation pattern has been highlighted for Crete in general (Agou et al., 2019; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012) as well as along the distribution range of *Z. abelicea* sites, with also an increase in temperature seasonality (Goedecke and Bergmeier, 2018). In our study, when we used the optimal number (according to the model) of 49 stations (i.e. all of the stations with available data for Crete for the concerned period) for the interpolation of precipitation amount, such a trend did not stand out. However, when we limited the number of weather stations to be taken into account for the interpolation of precipitation amount to the closest 10 weather stations (and we could discuss if 10 is already too much, considering the lack of stations situated in the mountainous areas as well as in eastern Crete), such a regional trend became visible (Fig. S4). Indeed, rainfall in most months, as well as annual rainfall were mostly distributed along the first axis of the principal component analysis which mirrors quite well the longitudinal position of the different mountain ranges and the general climatic patterns of the island and shows that the plots in the Levka Ori and Mt. Kedros receive more rain than those from Dikti and Thripti. Minimum, maximum and mean temperature varied instead along the second axis, which was more reflective of the altitudinal distribution of the plots. Our analysis allowed to distinguish well between mountain ranges. However, it is less precise when looking at data within a single mountain range. For example, a striking difference in precipitation records is found in the principal component analysis between plots situated in the western Levka Ori (Fokies, Machi and Xeropotamos) compared to those situated in the eastern Levka Ori (Impros and Niato) which seem to receive a lot more rain than the former. This is mainly due to their geographical proximity, albeit not on the same mountain side and therefore perhaps not being under the same precipitation regime, with a weather station situated at 715 m a.s.l. which shows one of the highest precipitation records of Crete. Therefore, due to the highly complex topography of the mountains, lee-side effects and the scarcity of weather stations in the mountains from the dataset used in this study, we think that at present there is too much uncertainty to assess with certainty and precision the precipitation variability within a given mountain range.

4.5. Major drivers of Zelkova abelicea growth

Although we investigated a fair amount of geographic, physiognomic, edaphic and climatic variables, only few revealed influential in explaining growth differences in *Z. abelicea.* None of the edaphic variables revealed significant in discriminating between *Z. abelicea* growth, showing that although some variability in soil conditions was observed, soil composition does not seem to play a crucial role in influencing *Z. abelicea* growth. Only longitude and rainfall in June, when keeping initial tree height constant, revealed significant in explaining differences in tree growth between plots (Fig. 4). 52% of the variation in the data was explained by the model, while longitude alone, or more generally speaking geographical position on the island since the plots are situated on a west to east line, was the variable which explained the highest proportion of variation (22%). June precipitation explained 7% of the variation in the data while the union of June precipitation and longitude explained a further 9%, pointing towards the fact that both variables explain partly the same structures (i.e. tree growth variations) and that both are correlated.

In Crete, as for most of the Mediterranean region, a large part of precipitation falls during the winter months, with low to null rainfall during the summer season (Agou et al., 2019; Koutroulis et al., 2010, 2013), while only 20% of precipitation is estimated to fall during the springtime (Koutroulis et al., 2013). *Zelkova abelicea* as well as its Sicilian relative, *Z. sicula* Di Pasquale, Garfì & Quézel, seem to not be able to fully exploit the abundant winter precipitation. In fact, during the winter, the deciduous *Zelkova* trees are dormant, and thus most of the winter rainfall is ineffective to growth as it is lost to runoff, infiltrated too deep, or evaporated by the time the trees come out of winter dormancy (Garfì, 1997a; Fazan et al., 2017). Therefore, late spring and early summer precipitation and temperature have been proven to be crucial for the growth of both *Z. abelicea* (Fazan et al., 2017) and *Z. sicula* (Garfì, 1997a). Actually, spring or summer precipitation and temperature are critical for determining growth in the Mediterranean context before the onset of the summer drought period and consequent growth reduction or cessation. Many dendrochronological investigations (e.g. Tessier et al., 1994, Hughes et al., 2001, Cherubini et al., 2003, Griggs et al., 2007, Campelo et al., 2009, Di Filippo et al., 2010, Nijland et al., 2011, Lebourgeois et al., 2012, Touchan et al., 2014, Papadopoulos, 2016, Fyllas et al., 2017) have shown that the growth of several other Mediterranean tree species is correlated positively with late spring or summer water availability and precipitation or negatively with temperature.

Initial tree height was responsible for explaining 5% of the variation found in tree growth but did not co-vary with longitude or June precipitation (0.6%, respectively 0%). Indeed, no longitudinal trend was found in initial tree height. However, significant differences did occur between mountain ranges. The fact that trees from Mt. Kedros are significantly taller than elsewhere, is most probably related to the sampling procedure (i.e. only 4 plots were sampled there and all had an average initial tree height above 100 cm) but it cannot be excluded that this pattern could also be related to differences in browsing pressure and browsing history. Trees from Dikti and Levka Ori displayed a similar height pattern, and both had plots showing a wide variety of initial tree heights (Table 1). Trees from Thripti, however, had significantly smaller initial tree heights than plots from all other mountain ranges. This is consistent with the findings of Kozlowski et al. (2014) who recorded no tall, well-developed trees in Thripti. The fact that trees from Thripti are confirmed to be smaller than elsewhere could be related to climatic constraints on the growth of this easternmost *Z. abelicea* population, as previously mentioned also for shoot elongation.

The fact that longitude was the variable that explained the highest proportion of variance, and not one of the climatic, edaphic or physiognomic variables shows that we were not able to find exactly which variable(s) explain(s) the observed differences in *Z. abelicea* growth between mountain ranges. Precipitation in specific months seem to be a good candidate, as shown above, although longer records and a less scanty network of weather stations would be needed to further investigate this point. Finally, we cannot rule out the roles of genetic variation, browsing history and browsing patterns in influencing *Z. abelicea* growth. Indeed, Christe et al. (2014) showed that *Z. abelicea* trees were genetically different on each mountain range. Although browsing history and patterns were never analyzed for *Z. abelicea* sites, several authors have shown the influence of land use or browsing history on tree growth or stand structure in the Mediterranean (e.g. Chauchard et al., 2007, Cierjacks and Hensen, 2004, Linares et al., 2010, Plieninger, 2007). Therefore, growth patterns may also be determined or influenced by the genetic background of the trees as well as the browsing history and patterns of the different sites.

4.6. Implications for conservation and outlook

When browsing is removed, *Z. abelicea* trees of the Levka Ori and Mt. Kedros grow more than trees from Dikti and Thripti. The former are able to grow on average twice as much in the same amount of time than the latter, and therefore it will take them on average half the time of the latter to grow out of the reach of goats. Some discrepancies do exist amongst plots within a mountain range (e.g. NIA1 and IMB1 plots have very low growth in comparison with all the other Levka Ori plots), which can probably be explained by local site specificities, differences in former land-use management or genetic factors. Nevertheless, the fact that trees from eastern Crete grow at lower rates is important to consider when planning and implementing conservation actions.

In addition, no study has yet investigated why Thripti is currently devoid of fruiting individuals (see also Kozlowski et al., 2014) while they are present in varying amounts in most other sites further west. One could hypothesize that this could be due to the presence of younger, i.e. not yet mature, *Z. abelicea* individuals than elsewhere, which could also be supported by the fact that this population was only discovered by the scientific community during the second half of the 20th century (Kozlowski et al., 2014). However, such an assumption seems unsubstantiated as Christe et al. (2014) show an ancient colonization of Crete by *Z. abelicea,* also in eastern Crete, occurring already before the early Miocene, as well as an absence of effective gene flow mediated by seeds between mountain ranges perhaps already since the Miocene. The remoteness of the site and the rarity of *Z. abelicea* individuals in that area probably explains why the population was discovered only recently. Goedecke and Bergmeier (2018) hypothesize that a gradient of less favourable climatic conditions from west to east explains why populations may be more scattered with a higher proportion of dwarfed trees more to the east. Our results go in that direction by showing that precipitation patterns, and more precisely the seemingly critical precipitation of the month of June decrease eastwards and are the lowest in Thripti, hence affecting the growth rate, the maximum potential size and sexual reproductive ability of trees, in addition to the omnipresent browsing pressure. Therefore, the absence of well-developed, large and/or fruiting individuals (at present) in Thripti can mainly be imputable to constraining environmental conditions and not to higher than elsewhere browsing patterns. For conservation reasons, it is important to assess if it is possible under current (and future) climatic conditions to have sexually reproducing individuals in Thripti, as well as if they once existed in the past. Although it is more than the scope of the current study to answer the first question, Christe et al. (2014) give some clues to answer the second. Indeed, they found high levels of variability in chloroplast markers for each studied population, including Thripti, which indicates that the population is composed of several distinctly genetically different individuals. Such a diversity must have arisen through sexual propagation and not from vegetative, genetically uniform, root suckers, which the species is able to produce profusely (Egli, 1997; Fazan et al., 2012; Kozlowski et al., 2012; Søndergaard and Egli, 2006). This assumption indeed, is consistent with the behaviour of the congeneric *Z. sicula* on Sicily, in which fruiting was observed for the first time even on dwarfed trees, constrained strongly by climatic factors in their current natural range, but only after grazing had been excluded for a few years (Garfì, 1997a).

According to all the issues addressed above, and in the view of a long-term conservation planning, the easternmost populations should deserve a special concern with respect to grazing management. Due to the assumed environmental constraints, at the state of our knowledge, it is not possible to foresee if *Z. abelicea* individuals from Thripti will ever reach the size of fully developed arboreal trees or even grow enough to surpass a browsing height threshold. However, the reorganization of grazing activities towards a greater sustainability, involving sufficiently long periods of protection from browsing pressure on a rotational basis could eventually promote fructification and seedling establishment and therefore allow a demographic increase of those populations and the preservation of the high genetic variability found within the species.

5. Conclusions

Knowing how overbrowsed trees grow across their distribution range when browsing is removed and knowing what factors drive growth are important to consider when planning conservation actions and when looking at grazing management options. In our study, we found that *Z. abelicea* trees from eastern Crete grew twice less in the same period than trees from central and western Crete. These findings were put in relation with precipitation patterns, and in particular the crucial spring and early summer precipitation. Previous studies have also shown the strong influence of overbrowsing on *Z. abelicea* growth overall. In order to avoid the extinction or shrivel of the most marginal stands, and in order to promote regeneration, a drastic shift in the way pastoral activities are currently carried out is necessary. More sustainable and extensive practices would help to maintain population size and promote regeneration while at the same time keeping the high genetic variability found within the species. In the light of our recent findings, special attention should therefore be given to the eastern *Z. abelicea* populations to allow sufficient time and resources for protection or regenerative measures to be effective.

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CRediT authorship contribution statement

LF conceived the study, DG and IR carried out field measurements, TN analyzed soil samples in the laboratory, LF performed the statistical analyses, LF wrote the manuscript, LF, SP, GG and GK reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02031.

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Supplementary material

Table S1. List of the 49 weather stations of Crete with available data between October 2014 and September 2020, provided by the Environmental Research Institute of the National Observatory of Athens (NOA) (Lagouvardos 2017) and available online (meteosearch.meteo.gr). The stations are listed according to their longitudinal position from west to east. The code refers to the NOA station code. The start date gives the first month and year for which data was available within the studied period. More information can be found online at http://meteosearch.meteo.gr

Name	Prefecture	Code	Latitude (DD)	Longitude (DD)	Altitude (m a.s.l.)	Start date
Falasarna	Chania	LGL9	35.49	23.58	10	<10.2014
Elos	Chania	LG2C	35.36	23.64	535	12.2014
Palaiochora	Chania	LG36	35.23	23.68	3	<10.2014
Kandanos	Chania	LG9G	35.33	23.74	430	07.2016
Zymvragou	Chania	LG0O	35.44	23.76	296	05.2019
Kakopetros	Chania	LG7R	35.42	23.76	462	12.2019
Kolympari	Chania	LG5H	35.52	23.80	40	11.2016
Sempronas	Chania	LG9D	35.38	23.82	640	06.2015
Platanias	Chania	LG3E	35.52	23.88	12	07.2015
Alikianos	Chania	LGT4	35.45	23.91	95	<10.2014
Samaria park	Chania	LGB4	35.31	23.92	1250	<10.2014
Stalos	Chania	LG1N	35.50	23.93	93	10.2018
Samaria gorge	Chania	LGY1	35.29	23.96	349	<10.2014
Chania center	Chania	LGN3	35.51	24.01	7	<10.2014
Sfakia	Chania	LGW4	35.23	24.02	770	<10.2014
Chania south	Chania	LG7Q	35.49	24.03	67	07.2020
Chania	Chania	LG25	35.53	24.07	137	<10.2014
Agioi Pantes	Chania	LG7E	35.40	24.15	148	10.2015
Askyfou	Chania	LGZ6	35.29	24.18	715	<10.2014
Vrysses	Chania	LG70	35.38	24.20	58	<10.2014
Asi Gonia	Chania	LG6J	35.27	24.29	380	09.2017
Plakias	Rethymno	LGT2	35.19	24.39	5	<10.2014
Rethymno city	Rethymno	LG4I	35.36	24.49	50	03.2017
Rethymno	Rethymno	LG58	35.37	24.47	39	<10.2014
Spili	Rethymno	LG75	35.22	24.54	405	<10.2014
Fragma Potamon	Rethymno	LGD4	35.28	24.57	240	<10.2014
Fourfouras	Rethymno	LGL1	35.21	24.71	471	<10.2014
Moires – Petrokefali	Irakleio	LGI2	35.03	24.83	54	<10.2014
Anogeia	Rethymno	LGB6	35.29	24.89	801	<10.2014
Lentas	Irakleio	LGP0	34.93	24.92	15	<10.2014
Gortyna	Irakleio	LG9K	35.06	24.94	185	03.2018
Plora	Irakleio	LG8N	35.01	24.94	132	01.2019
Vagionia	Irakleio	LG7B	35.01	25.00	196	12.2014
Stavrakia	Irakleio	LG8B	35.25	25.06	245	12.2014
Irakleio west	Irakleio	LGW2	35.31	25.08	85	<10.2014
Irakleio port	Irakleio	LG61	35.34	25.13	10	<10.2014
Metaxochori	Irakleio	LGD7	35.13	25.14	418	<10.2014
Irakleio	Irakleio	LG30	35.30	25.16	115	<10.2014
Irakleio east	Irakleio	LG2F	35.33	25.16	35	01.2016
Pyrathi	Irakleio	LG8A	35.10	25.19	311	<10.2014
Peza	Irakleio	LG0K	35.21	25.20	305	04.2018
Tzermiadon	Lassithi	LG50	35.20	25.49	820	<10.2014
Potamoi	Lassithi	LG9N	35.21	25.53	865	03.2019
Neapoli	Lassithi	LG4O	35.26	25.61	265	04.2019
Finokalia	Lassithi	LG9A	35.33	25.67	250	10.2014
Agios Nikolaos	Lassithi	LGJ9	35.19	25.72	15	<10.2014
Ierapetra	Lassithi	LG95	35.01	25.75	5	<10.2014
Siteia	Lassithi	LGM2	35.20	26.10	30	<10.2014
Moni Toplou	Lassithi	LG4P	35.22	26.22	170	07.2019

Table S2. Leave-one-out cross validation statistics for the interpolation procedure for the 49 weather stations with available data for the period October 2014 to September 2020. Optimal parameters α (Gaussian shape parameter) and N (number of stations) (see De Cáceres et al. 2018 and De Cáceres & Granda 2021 for details) for minimum, maximum temperature and precipitation amount optimal α was 0.5 and N was 49. For precipitation occurrence optimal α was 2.5 and N was 3. n: number of stations or number of days, r: linear correlation coefficient, MAE: mean absolute error. SD stations: standard deviation of MAE across stations, SD days: standard deviation of MAE across days. Date rainfall: sum of precipitation across stations for each date. Date precipitation stations: number of stations with precipitation events for each date.

			MAE			Bias		
Variable	n	r	Value	SD stations	SD days	Value	SD stations	SD days
Minimum temperature (°C)	84991	0.90	2.23	0.97	0.42	-0.02	2.28	0.07
Maximum temperature (°C)	84972	0.95	1.64	0.83	0.32	0.01	1.56	0.06
Temperature range (°C)	84969	0.57	2.25	1.06	0.67	0.03	2.21	0.09
Station annual rainfall (mm·yr^{-1})	49	0.66	1405.93	1290.85	NA	97.83	1916.85	NA
Station precipitation days	49	0.47	92.00	80.91	NA	-9.39	122.78	NA
Date rainfall (mm)	1429	0.99	7.55	NA	18.54	3.40	NA	19.73
Date precipitation stations	1429	0.99	1.15	NA	1.26	-0.21	NA	1.69

Figure S1. Principal component analysis of geographical parameters of *Z. abelicea* fenced plots. The 1st axis represents 52% of the variation and the 2nd axis represents 27%. A. Distance biplot (scaling 1): the distance between plots approximates their Euclidean distances in a multidimensional space. Scaling 1 allows to see differences amongst plots. B. Correlation biplot (scaling 2): the angles between descriptors reflect their correlation. Projecting a plot at right angle on a descriptor approximates the position of the plot along that descriptor (see Borcard et al. 2011 for more details). Plots are represented by the colored symbols and differentiated between mountain ranges (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti), while descriptors (variables) are represented by grey arrows.

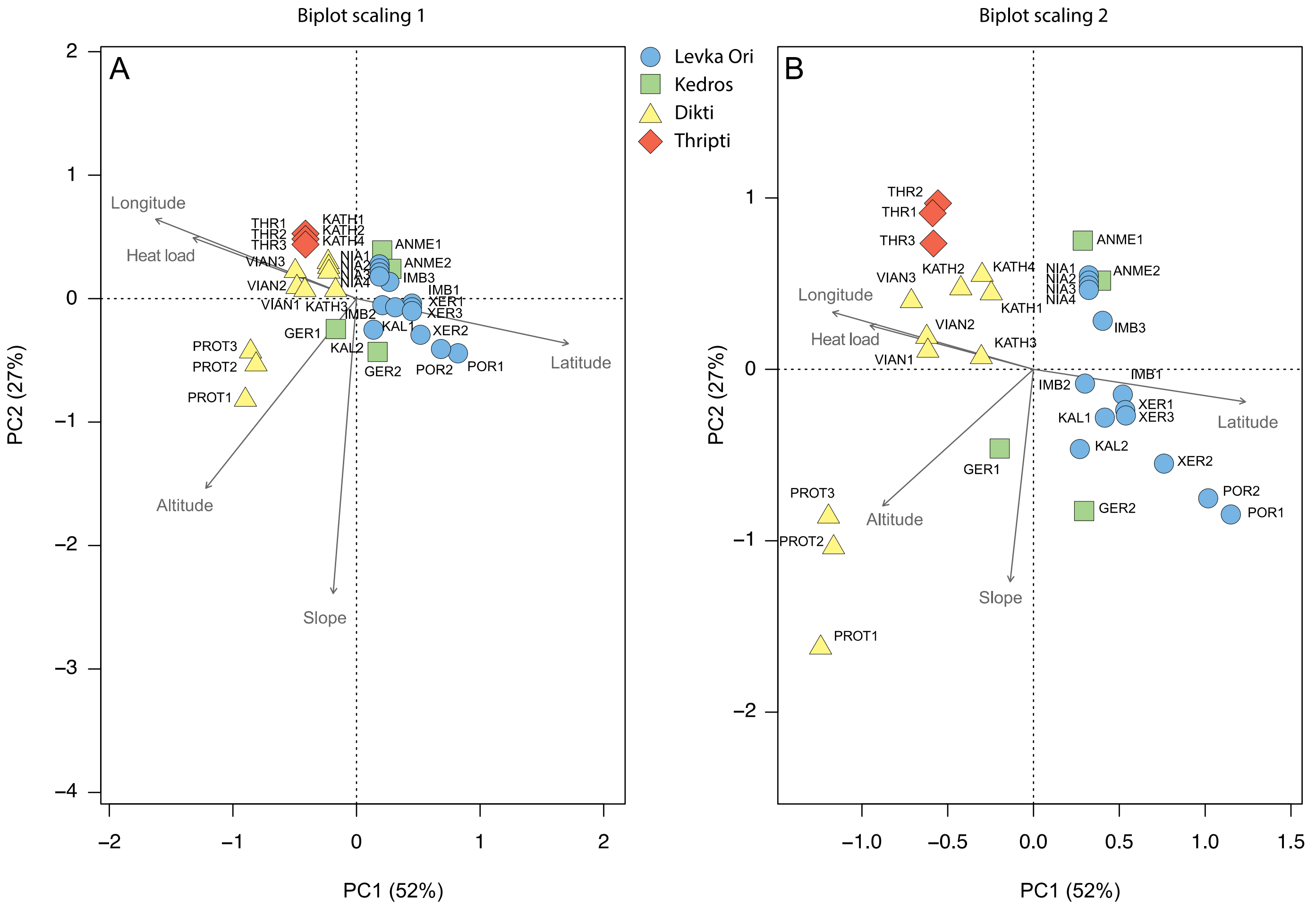

Figure S2. Principal component analysis of the soil parameters. The 1st axis represents 36% of the variation the 2nd axis represents 18%. A. Distance biplot (scaling 1): the distance between plots approximates their Euclidean distances in a multidimensional space. Scaling 1 allows to see differences amongst plots. B. Correlation biplot (scaling 2): the angles between descriptors reflect their correlation. Projecting a plot at right angle on a descriptor approximates the position of the plot along that descriptor (see Borcard et al. 2011 for more details). Plots are indicated by colored symbols and distinguished between mountain ranges (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti), while descriptors (variables) are represented by grey arrows. El. cond: electrical conductivity, Org. mat: organic matter.

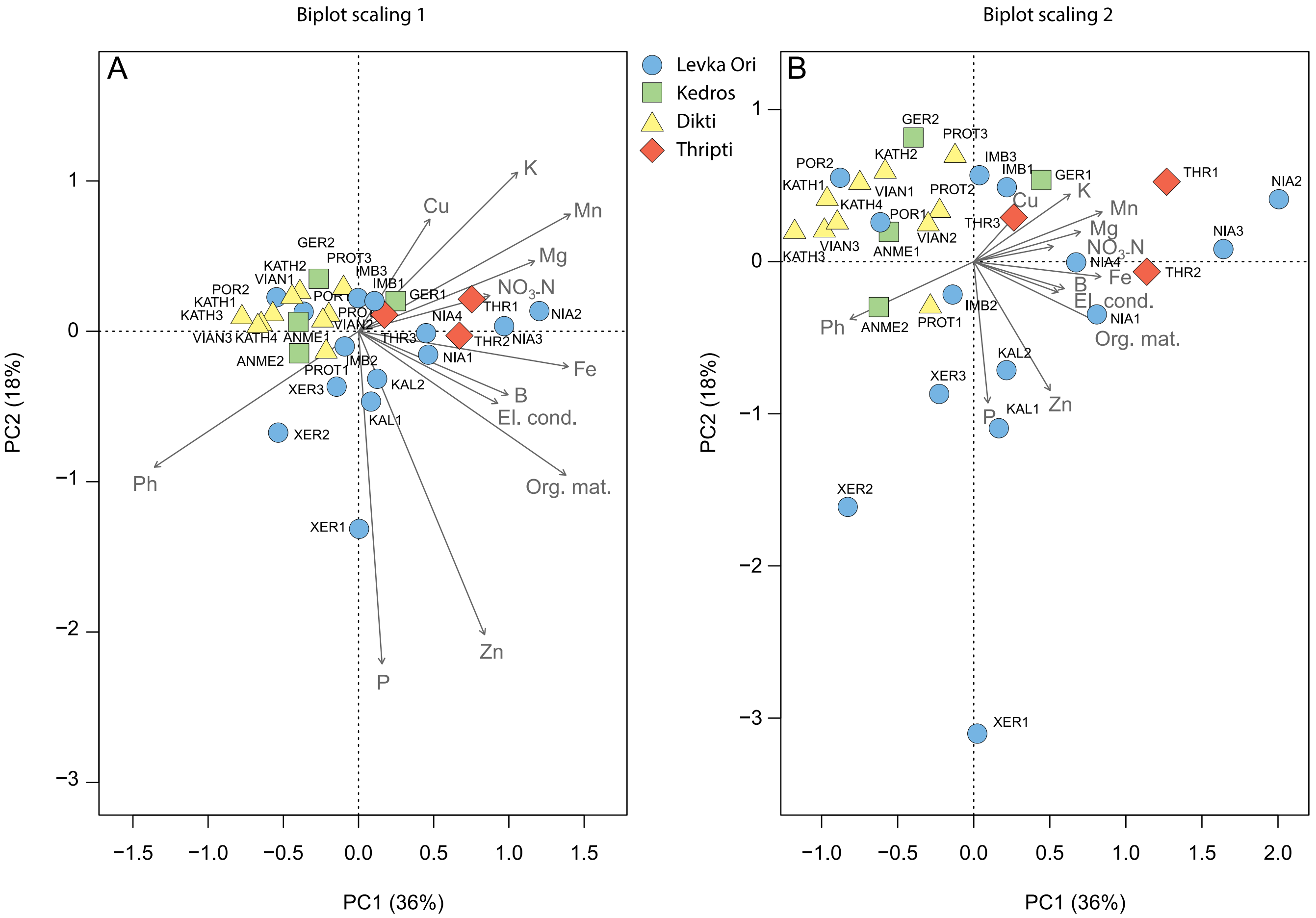

Figure S3. Soil textures of each of the 31 fenced plots. The soil texture diagram follows the USDA soil texture classification (Soil Science Division Staff 2017). Soil particles are separated into three classes (clay, silt, sand) according to size: sand <2 µm, silt: 2-50 µm, sand: 50 µm-2 mm. The relative proportion of each class gives an indication of their belonging to one of 12 soil texture classes. Soil texture class abbreviations: Cl: clay, SiCl: silty clay, SaCl: sandy clay, ClLo: clay loam, SiClLo: silty clay loam, SaClLo: sandy clay loam, Lo: loam, SiLo: silty loam, SaLo: sandy loam, Si: silt, LoSa: loamy sand, Sa: sand. Plots are indicated by colored symbols and distinguished between mountain ranges (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti).

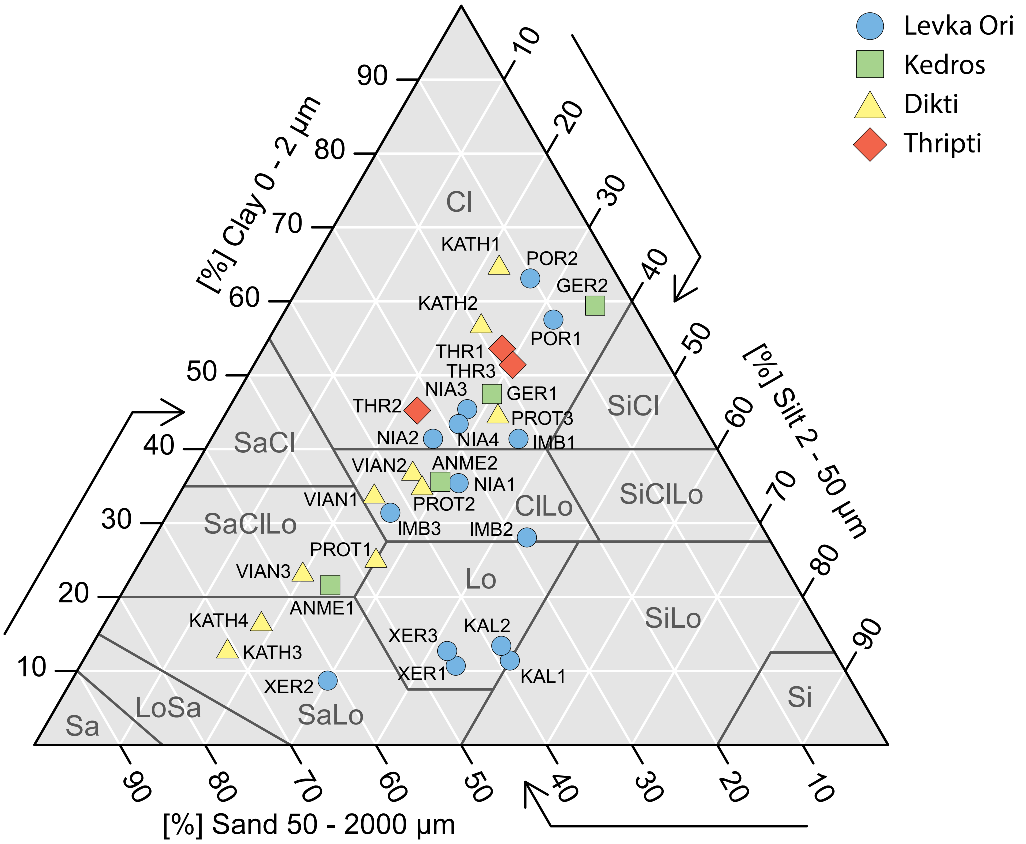

Figure S4. Principal component analysis of interpolated weather data for the 31 *Z. abelicea* fenced plots. Mean, minimum and maximum yearly (previous October to current September) average temperature as well as yearly average precipitation for the period October 2014 to September 2020 are given. In addition, monthly average precipitation are given. The 1st axis represents 62% of the variation and the 2nd axis represents 30%. A. Distance biplot (scaling 1): the distance between plots approximates their Euclidean distances in a multidimensional space. Scaling 1 allows to see differences amongst plots. B. Correlation biplot (scaling 2): the angles between descriptors reflect their correlation. Projecting a plot at right angle on a descriptor approximates the position of the plot along that descriptor (see Borcard et al. 2011 for more details). Plots are indicated by colored symbols and distinguished between mountain ranges (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti), while descriptors (variables) are represented by grey arrows. The small-lettered p in front of a month means previous year.

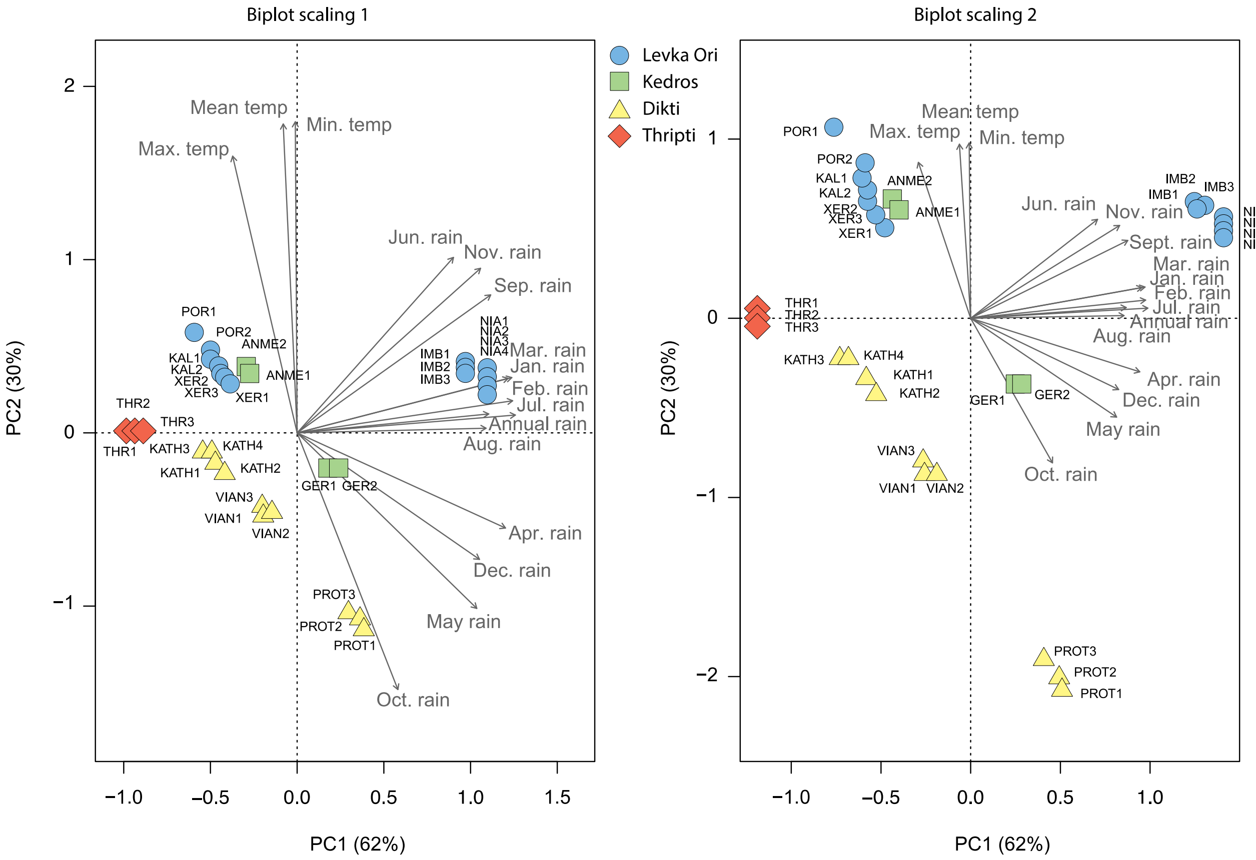

Table S3. Permutation test results for the redundancy analyses. Separate analyses were carried out for each of the four datasets (physio: tree physiognomy variables, geo: geographical variables, soil: soil proprieties variables, weather: interpolated weather variables). Model results including all variables (full) as well as parsimonious (parsi) model results are given below. The final model result is the combination of the significant variables of the datasets after permutation tests and forward selection. Significant p≤0.05 values are given in bold.

Dataset			Df	Variance	F statistic	Probability (>F)
Physio		Global model	1	0.36	4.86	**0.04**
		Residual	22	1.64	-	-
Geo	Full	Global model	5	1.11	4.49	**0.005**
		Residual	18	0.89	-	-
		Constrained axis 1	1	1.10	25.86	**0.007**
		Constrained axis 2	1	0.02	0.35	1.00
		Residual	21	0.89	-	-
	Parsi	Global model	1	0.88	17.37	**0.001**
		Residual	22	1.12	-	-
Soil	Full	Global model	12	1.30	1.70	0.18
		Residual	11	0.70	-	-
		Constrained axis 1	1	1.24	37.00	0.18
		Constrained axis 2	1	0.06	1.87	1.00
		Residual	21	0.70	-	-
Weather	Full	Global model	13	1.45	2.03	0.10
		Residual	10	0.55	-	-
		Constrained axis 1	1	1.41	53.99	0.11
		Constrained axis 2	1	0.04	1.44	1.00
		Residual	21	0.55	-	-
	Parsi	Global model	1	0.56	8.45	**0.008**
		Residual	22	1.44	-	-
Final		Global model	2	0.81	9.72	**0.002**
		Residual	20	0.83	-	-
		Constrained axis 1	1	0.79	19.04	**0.004**
		Constrained axis 2	1	0.02	0.40	0.56
		Residual	20	0.83	-	-

CHAPTER 3

TRAIT VARIABILITY IN DIASPORES AND FRUITS OF *ZELKOVA ABELICEA* (ULMACEAE) ACROSS ITS DISTRIBUTION RANGE

Laurence Fazan, Daniele Certini, Salvatore Pasta, Ilektra Remoundou, Dany Ghosn, Giuseppe Garfì, Gregor Kozlowski

Author contributions: LF conceived the study, LF, GG, SP collected field data and material, LF and SP prepared material for analysis, LF performed the statistical analyses, LF wrote the manuscript, LF, DC, SP, IR, DG, GG and GK reviewed the manuscript.

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Trait variability in diaspores and fruits of *Zelkova abelicea* (Ulmaceae) across its distribution range

Laurence Fazan[a,*], Daniele Certini[b], Salvatore Pasta[c], Ilektra Remoundou[d], Dany Ghosn[d], Giuseppe Garfi[c], Gregor Kozlowski[a,e,f]

[a] *Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, 1700, Fribourg, Switzerland*
[b] *School of Engineering, Institute of Energy Systems, University of Edinburgh, Sanderson Building, Robert Stevenson Road, Edinburgh, EH9 3FB, United Kingdom*
[c] *Institute of Biosciences and BioResources, National Research Council, Corso Calatafimi 414, 90129, Palermo, Italy*
[d] *Department of Geoinformation in Environmental Management, CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100, Chania, Greece*
[e] *Natural History Museum Fribourg, Chemin du Musée 6, 1700, Fribourg, Switzerland*
[f] *Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, 3888 Chenhua Road, Songjiang, 201602, Shanghai, China*

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ABSTRACT

In the tree genus *Zelkova* (Ulmaceae), diaspores show a unique morphology amongst woody angiosperms. Shoots with leaves and fruits detach and act as flying dispersal units. Surprisingly little attention has been given to these structures, and it is unknown whether the characteristics of these diaspores vary amongst species or within the range of a single species. The endemic Cretan *Z. abelicea* (Lam.) Boiss. is one of two *Zelkova* species occurring at the western end of the distribution range of the genus. This relict species grows in a typical Mediterranean climate, in conditions completely different from the warm and moist climate that occurred during the apogee of the genus in the Paleogene, or that are still found for the three East Asiatic species of the genus. Here we studied for the first time the characteristics of diaspores, including fruit traits, of *Z. abelicea* across the whole range of the species. We showed that most traits are very variable amongst individual trees but less so between mountain ranges and that only diaspore stem length and proportion of sound seeds per diaspore and per tree vary significantly amongst mountain ranges. We showed that trees from central and eastern Crete produce extremely low to null proportions of sound seeds and that those trees oftentimes are smaller and have shorter diaspores with less leaves and fruits. Furthermore, we found that diaspores that were severely affected by a gall midge species (Cecidomyiidae) produced less fruits, but that seed soundness was not significantly impacted by the presence or absence of the galls. The very low proportion of sound seeds found in central and eastern Crete raises concern about the long-term persistency and regeneration of the species in those areas.

1. Introduction

The seed dispersal units (hereafter called diaspores) of the species within the genus *Zelkova* are unique among angiosperms (Certini et al., 2020; Hoshino, 1990). The diaspore is an annually produced shoot specialised in flowering and dispersal and is morphologically different from the non-flowering, perennial shoots (see Hoshino, 1990 for details). On this unit, leaves and flowers (male, female, hermaphrodite) and subsequently fruits are produced (Fig. 1A). Fruits are generally found in the axil of the alternate leaves (usually one fruit per axil) and closer to the top of the unit due to a clear zonation of flower sex on the shoots with clusters of caducous male flowers being proximal, usually solitary hermaphrodite flowers being intermediate and solitary female flowers being distal. In autumn, the shoot abscises at the base and falls off with dried leaves and fruits, i.e., the so-called diaspore (Fig. 1B). In the genus *Zelkova*, dispersal is mainly through wind (anemochory) and gravity (barochory) (L. Fazan, *pers. obs*; Egli, 1997; Hoshino, 1990; Oyama et al., 2018), but zoochory has also been reported for the East Asiatic *Z. serrata* as macaques eat fresh fruits (Nakagawa, 1990; Tsuji and Takatsuki, 2004). For *Z. abelicea* (Lam.) Boiss., secondary dispersal (diplochory) has been observed through ants transporting fallen fruits to their nests (L. Fazan, G. Garfi & S. Pasta, *pers. obs.*; Egli 1997). The genus

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* Corresponding author. Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, 1700, Fribourg, Switzerland.
E-mail addresses: laurence.fazan@unifr.ch (L. Fazan), d.certini@ed.ac.uk (D. Certini), salvatore.pasta@ibbr.cnr.it (S. Pasta), hlektra@maich.gr (I. Remoundou), dghosn@maich.gr (D. Ghosn), giuseppe.garfi@ibbr.cnr.it (G. Garfi), gregor.kozlowski@unifr.ch (G. Kozlowski).

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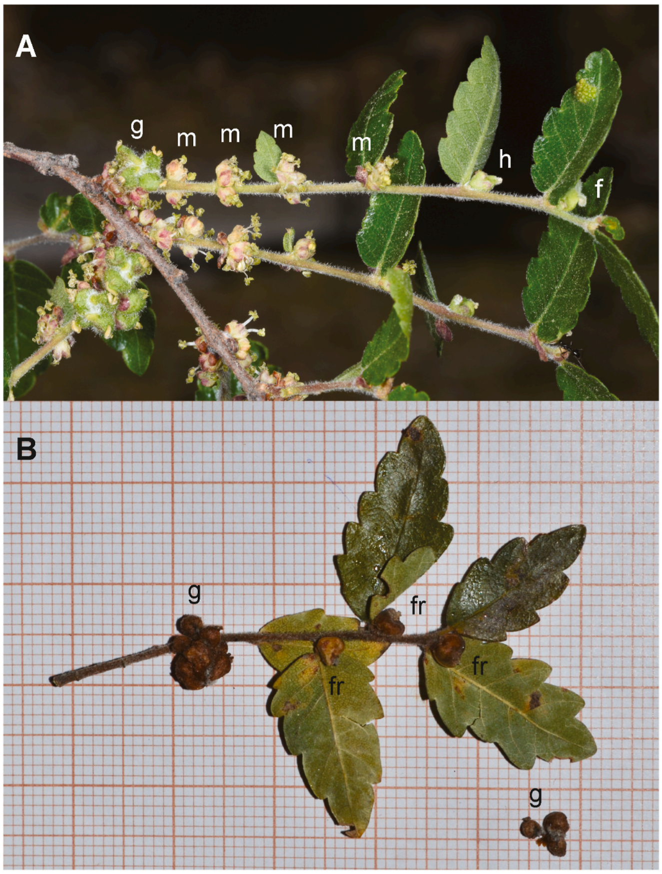

Fig. 1. A. Flowering shoots of *Z. abelicea* with leaves, proximal male flowers with (g) or without galls (m), intermediate hermaphrodite flower (h) and distal female flower (f). B. diaspore of *Z. abelicea* with leaves, galls (g) and fruits (fr). Pictures: E. Kozlowski (A), S. Pasta (B).

is characterised by a bimodal dispersal scheme. Fruits disperse either attached to the diaspore or as single fruit that detach and fall off (Certini et al., 2020; Oyama et al., 2018).

The genus *Zelkova* is a climate relict with a north Pacific (Burnham, 1986) or north-eastern Chinese (Zhang et al., 2017) origin that thrived under warm and humid climatic conditions. The genus was widespread throughout the Northern Hemisphere during most of the Paleogene. Due to the dramatic climatic changes during the late Miocene and early Quaternary, the distribution range of the genus drastically shrunk so that it is now found and restricted to two disjunct refugial areas and includes six extant species (Kozlowski and Gratzfeld, 2013). Three are located in south-eastern Asia, namely *Z. serrata* (Thun.) Makino, *Z. schneideriana* Hand.-Mazz. and *Z. sinica* C.K. Schneid., where they thrive under temperate and humid climates with no summer drought (Garfì et al., 2021). The remaining three species are found in southwestern Eurasia. *Z. carpinifolia* (Pall.) K. Koch grows in the Transcaucasian and Middle East regions under almost constant moist conditions with a very short dry summer season (Garfì et al., 2021; Kvavadze and Connor, 2005). The two remaining species are restricted to the Mediterranean area. *Z. sicula* Di Pasq., Garfì & Quézel is endemic to the Italian island of Sicily and *Z. abelicea* is endemic to the Greek island of Crete. The two Mediterranean *Zelkova* species occur in areas with climatic conditions distinct from the other extant *Zelkova* species, characterised by three to four months of pronounced summer drought.

Little is known about diaspore and fruit traits within the *Zelkova* genus. Although being mainly descriptive, such trait studies are of high importance as they may yield essential knowledge about the dispersal capacities, seed soundness and regeneration potential of the studied species. They provide basic information on traits that may play a key role in future comparative studies and are important to detect potential intraspecific changes in species located in areas subject to rapidly changing environmental conditions, which is the case for the two Mediterranean *Zelkova* species (Cos et al., 2022; Giorgi and Lionello 2008; Lionello et al., 2014). In addition, studying trait variation across the range of the species may put into light unseen or hidden trends or patterns that may be of importance for both the survival and the conservation of a species (Westerband et al., 2021). Moreover, several *Zelkova* species have been recorded as having low to null natural regeneration. This fact has important conservation implications, leading to the classification of all but one species of the genus as threatened on the IUCN Red List of Threatened Species (Bétrisey et al., 2018a, 2018b, 2018c; Garfì et al., 2017; Kozlowski et al., 2012; Song et al., 2018).

Characteristics of diaspores of *Z. abelicea* have only been partially described by Jasińska et al. (2015, 2021) who studied leaf morphology of the three westernmost species, while Certini et al. (2020) investigated the flight behaviour of *Z. abelicea* diaspores. Seed soundness of the latter species, despite being crucial for plant propagation actions within conservation projects, has only been described from a low number of trees and mainly from a small portion of the range of the species (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007).

The response of plant species in constraining environments can involve significant failure or ineffectiveness of sexual regeneration or propagation, as is the case with species living at the edge of the distribution range of their genus (Garfì et al., 2021). Therefore, in this paper, we describe and study for the first time several traits of the diaspores and of the fruits of *Z. abelicea* across its entire distribution range in order to 1) evaluate the characteristics of different traits of the diaspores and of the fruits and any possible variation across the range of the species, 2) assess seed soundness at a species, mountain and tree level, and 3) check for possible explanations of the spatial variability of the investigated traits. The results of our study are of high importance to improve knowledge about the dispersal and sexual reproductive performance of this threatened relict tree species in view of future implementation of conservation efforts.

2. Material and methods

2.1. The species

Zelkova abelicea is a monoecious, broadleaved tree. The species grows in all mountainous areas of Crete between 800 and 1800 m a.s.l. in woodland communities in supra- and oro-Mediterranean climatic conditions with mean annual temperatures of ca. 9.3–12.7 °C, and up to 1100–1600 mm of precipitation in the rainiest areas (Fazan et al., 2017; Ghosn et al., 2010). The species has been assessed as Endangered (EN) on the IUCN Red List of Threatened Species (Kozlowski et al., 2012) and is threatened throughout its range mainly with intense and localized caprine and ovine pastoralism, causing overbrowsing, trampling and associated soil erosion and environmental degradation (Egli, 1995, 1997; Fazan et al., 2012; Fournaraki and Thanos, 2006; Kozlowski et al., 2018; Søndergaard and Egli, 2007). Overbrowsing by goats hinders tree growth and keeps individuals in a stunted dwarf-like form (Fazan et al., 2012). Dwarfs cannot produce fruits and are only able to propagate asexually via root suckers, which the species does profusely, especially when disturbance occurs (Egli, 1997; Fazan et al., 2012; Kozlowski et al., 2018). Only trees that have grown tall enough to escape browsing produce fruits. Fruiting trees are estimated to make up only ca. 5% of all *Z. abelicea* individuals (Kozlowski et al., 2014). Fruit production follows a masting behaviour with massive and widespread fruit production every two to three years (L. Fazan, *pers. obs.;* Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007). The proportion of fruits with sound seeds is highly fluctuant, and has been reported to be ranging from 0% to 56% depending on the sampled tree, locality, and year of collection (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007), but has not been systematically studied throughout the range of the species. Pre-dispersal seed predation has never been reported up to the present. However, trees in several localities were noticed to have galls made by gall midges (family: Cecidomyiidae, class: Diptera) on the male flowers (L. Fazan, *pers. obs.*) and it is unknown whether this may influence fruit quantities, seed soundness or other diaspore traits. Seedling survival in the wild is low at best, supposedly due to adverse conditions (e.g. browsing, summer drought). However, hundreds of seedlings have been propagated in forest nurseries over the past few years in the scope of local conservation projects (Abelitsia, 2021; Zelkova, 2021).

2.2. *Plant material collection and preparation*

Thirty-seven fruiting trees were randomly sampled throughout the distribution range of *Z. abelicea* (Fig. 2) in October 2017, i.e. during a masting year when numerous *Z. abelicea* trees bore fruits. This was not the case in the preceding and subsequent years in which only a few trees were found to bear fruits (L. Fazan, *pers. obs.*). Twenty-four trees were sampled in the Levka Ori, three trees on Mt. Psiloritis and ten trees on Mt. Dikti, reflecting the natural distribution of *Z. abelicea* populations throughout its range (Kozlowski et al., 2014). The easternmost mountain, namely Thripti, was not sampled because it does not host at present any flowering trees and Mt. Kedros was not visited. The geographic position and altitude of each tree are found in Table S1 in the Supplementary Material.

Fifteen diaspores (Fig. 1B) were randomly handpicked from the sampled trees, except for one tree for which only 14 diaspores were sampled and one tree for which no diaspores were collected. The diaspores were then stored individually, as flat as possible, in paper envelops and left to dry for 4 months at room conditions (20 °C, 40–50% relative humidity). Each diaspore was then processed individually, and the following traits were measured or counted: number of leaves per diaspore, leaf length, leaf width, leaf area, leaf weight, diaspore stem length, number of fruits per diaspore and number of galls per diaspore. Leaf mass per area (LMA) was calculated as dry leaf mass divided by leaf surface and was computed for each leaf. Leaves were weighed on a Mettler Toledo AG204 analytical balance (Mettler, 2021). All other leaf measurements were done using Fiji of ImageJ2 (Rueden et al., 2017; Schindelin et al., 2012). The single-seeded fruits (Fournaraki and Thanos, 2006) found on the diaspores were opened to assess visually seed soundness and the proportion of sound seeds per diaspore (i.e. number of sound seeds compared to the total number of seeds of a given diaspore). Galls triggered by the presence of a previously unknown gall midge (family: Cecidomyiidae, class: Diptera; L. Fazan, *pers. obs.*) occur on male flower parts, on the otherwise caducous stamens that grow abnormally and become enlarged and persistent (Fig. 1). During spring, these galls host the insect larvae which then exit the galls before the onset of the summer season. Due to the persistency of galled flowers, galls are also found on, and dispersed with, diaspores in autumn (L. Fazan, *pers. obs.*; Planchon, 1873).

To have a more statistically robust estimation of seed soundness per tree (especially for trees in which seed soundness was extremely low), fruits were additionally collected for each tree using the method described in Proto and Zimbalatti (2015) and Sola-Guirado et al. (2014) for manual olive collection. The trees were beaten using a wooden stick and all fallen material was gathered on large collecting nets that had been placed under the trees. The collected material was then sorted and the fruits were separated from the remaining material (leaves, twigs, galls) by sieves (mesh sizes between 2 mm and 6.3 mm) and by using a column blower CB-1 (Agriculex 2018).

From the outside, fruits with sound or unsound seeds are indistinguishable. Fournaraki and Thanos (2002) have shown that fruits with sound seeds of *Z. abelicea* can be separated due to their heavier mass from the lighter fruits with unsound seeds in which the embryo has not developed. Therefore, to assess the proportion of sound seeds per tree, fruits were sorted according to their weight, separately for each tree, using a column blower following the methodology used by Fournaraki and Thanos (2006). From all the sorted fruits, an average of 37 sound (range: 2–93) and 43 unsound (range: 10–126) fruits per tree were weighed on a Mettler Toledo AG204 analytical balance (Mettler, 2021). To assess the accuracy of the column blower method, fruits were cut open to test for seed soundness (the exact number of weighed fruits per tree is presented in Table S1 in the Supplementary Material). All fruits were opened for trees with less than 40 (sound) fruits. The number of misplaced fruits (i.e., unsound within sound and vice-versa) amongst the opened fruits was used to give a rough estimate of the accuracy of this method. When opened, sound seeds had a developed, white, fleshy embryo beneath the seed coat, filling most of the fruit cavity. On the contrary, aborted, unsound seeds had an undeveloped shrunken seed or vestigial ovule that does not grow and most of the space within the fruit was empty (Fig. 3).

In addition, to see if tree size could influence diaspore and fruit traits,

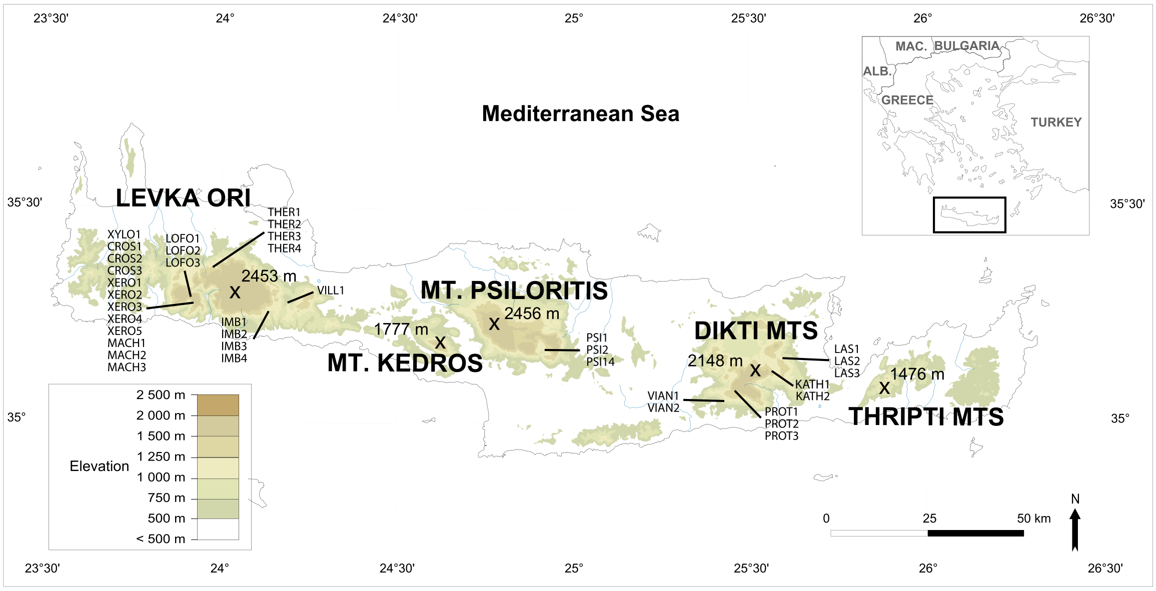

Fig. 2. Location of the 37 sampled trees in the five mountain ranges (Levka Ori, Mt. Kedros, Mt. Psiloritis, Dikti Mts. and Thripti Mts.) of Crete.

Fig. 3. Left: section of a fruit with a sound seed with a fleshy white viable embryo beneath the seed coat that occupies most of the available space. Right: section of a fruit with a small undeveloped and withered seed containing a non-viable or aborted embryo that does not fill up the fruit cavity.

trunk circumference at breast height was measured on each tree using a measuring tape, tree height was calculated using a clinometer and a measuring tape ("tangent method" described by Larjavaara and Muller-Landau, 2013), and canopy extension was estimated (i.e., the sum of canopy radii in 4 directions: north, east, south, west).

Table 1
Diaspore traits averaged for the 37 studied trees. # Lf: number of leaves, # Fr: number of fruits, Prop sfr: proportion of fruits with sound seeds, # Gl: number of galls, SL: stem length, LfL: leaf length, LfW: leaf width, LMA: leaf mass per area. NA: missing value. The overall median, mean, standard deviation (SD), minimum and maximum were computed directly over the raw unaveraged measurements.

Mt	Tree-ID	# Lf	# Fr	Prop sfr	# Gl	SL (mm)	LfL (mm)	LfW (mm)	LMA (mg/mm^2)
Levka Ori	XYLO1	4.7	2.7	0.13	0	31.50	18.42	10.58	0.12
	CROS1	4.0	0.4	0.67	3.60	20.85	12.46	8.04	NA
	CROS2	5.5	1.1	0.13	1.00	23.73	15.16	9.61	NA
	CROS3	5.7	2.1	0.28	0.20	42.87	17.70	10.84	NA
	XERO1	4.4	2.9	0.55	0.20	30.10	19.26	10.91	0.10
	XERO2	5.7	1.6	0.29	0.07	24.27	13.69	7.93	0.06
	XERO3	5.3	1.6	0.42	0	23.43	12.29	6.91	0.07
	XERO4	4.3	2.7	0.58	0	21.77	12.46	7.76	0.08
	XERO5	5.3	2.2	0.42	0.33	29.70	13.00	8.07	0.09
	MACH1	4.3	3.1	0.43	0.07	25.60	14.15	8.73	0.10
	MACH2	4.6	1.7	0.42	2.87	35.70	16.13	10.45	0.08
	MACH3	6.5	2.3	0.40	0.13	35.47	23.42	10.18	0.09
	LOFO1	4.1	1.3	0.26	1.13	20.47	15.83	9.41	0.06
	LOFO2	5.0	0.9	0.14	1.27	19.33	11.24	6.36	0.06
	LOFO3	3.2	1.0	0.20	0.73	18.73	12.69	8.38	0.06
	THER1	5.2	1.3	0.15	1.40	32.22	17.20	9.92	0.07
	THER2	3.6	0.5	0.38	2.47	26.46	16.92	9.48	0.07
	THER3	4.7	1.7	0.28	1.27	25.16	15.33	7.97	0.09
	THER4	4.1	1.4	0.38	4.13	23.64	12.88	7.64	0.09
	IMB1	2.9	2.5	0	0	28.27	17.99	9.22	0.08
	IMB2	4.3	1.9	0.03	0	29.50	18.09	9.59	0.06
	IMB3	NA	NA	NA	NA	NA	NA	NA	NA
	IMB4	4.7	2.5	0	0	31.66	17.10	8.83	0.10
	VILL1	4.4	1.5	0	0	19.06	18.98	10.32	0.09
Psiloritis	PSI1	4.6	1.7	0	0	14.93	15.48	9.37	0.08
	PSI2	4.5	2.3	0	0	18.63	17.51	10.44	0.09
	PSI14	4.2	1.8	0	0	10.59	15.14	9.27	0.08
Dikti	PROT1	5.7	3.1	0	0	23.03	12.61	8.35	0.09
	PROT2	4.3	2.5	0	0	19.29	16.18	10.03	0.10
	PROT3	5.5	3.4	0	0	25.26	13.13	8.88	0.08
	VIAN1	3.9	1.5	0	0	19.39	17.49	11.38	0.11
	VIAN2	4.1	1.3	0	0	27.18	17.37	10.52	0.10
	LAS1	3.7	1.2	0	0	12.97	11.84	7.01	0.08
	LAS2	3.7	1.1	0	0	14.14	13.39	8.04	0.08
	LAS3	4.5	1.2	0	0.57	20.50	18.01	10.99	0.08
	KATH1	4.9	1.4	0.14	0.40	21.06	13.72	7.37	0.09
	KATH2	4.5	1.1	0	6.47	25.50	14.57	8.90	0.12
Overall	Median	5.00	2.00	0.00	0.00	23.00	15.00	9.00	0.08
	Mean	4.57	1.79	0.18	0.79	24.26	15.56	9.10	0.08
	SD	1.26	1.00	0.33	1.85	8.60	4.78	2.67	0.02
	Minimum	1	0	0	0	6.00	3.00	2.00	0.01
	Maximum	8	6	1	13	65.00	36.00	19.00	0.18

2.3. Statistical analyses

All statistical analyses were done using R (version 4.0.2) (R Core Team, 2021). Kruskal-Wallis rank sum tests using function kruskal.test in package stats (R Core Team, 2021) were carried out to check for significant differences between trees and between mountain ranges of diaspore traits, as well as seed soundness, weight and size of individual trees. This test was also carried out to see if significant differences exist in the weight of fruits containing sound or unsound seeds. For traits that showed significant differences between mountains, pairwise Wilcoxon rank sum tests using function pairwise.wilcox.test of package stats (R Core Team, 2021) were carried out to assess more precisely which mountain ranges were significantly different.

Linear and generalised linear models with tree identity nested in mountain identity were used to partition the variation in diaspore traits, seed soundness and weight between trees and mountains. Function lmer of package lme4 (Bates et al., 2015) was used for continuous variables (leaf width, leaf length, LMA, stem length, fruit weight), while function glmer was used for count variables (family: Poisson, nb. of leaves, nb. of fruits and nb. of galls) and proportions of fruits with sound seeds per diaspore (family: binomial). Tree identity and mountain identity were used as random effects, specifying that tree identity was nested within mountain identity.

Spearman's rank correlation coefficients (Hollander and Wolfe, 1973) among diaspore traits as well as for the proportion of fruits with sound seeds per tree and fruit weight were computed using function cor in package stats (R Core Team, 2021) to assess relationships and the direction of the relationship between variables.

3. Results

3.1. Diaspore traits

Per tree summaries are presented in Table 1 and Supplementary Material Fig. S1, and trends per mountain are shown in the Supplementary Material Fig. S2. 58% of the investigated trees had sound seeds but only 18% of all the seeds attached to the diaspores were sound. The proportion of fruits with sound seeds per diaspore varied between 0 (only unsound seeds) and 1 (only sound seeds), but the average for diaspores with fruits containing sound seeds was 0.67. Significant variations were found in diaspore stem lengths (range: 6–65 mm, average: 24.26 mm), leaf lengths (range: 3–36 mm, average: 15.56) and leaf widths (range: 2–19 mm, average: 9.10 mm). LMA varied between 0.01 and 0.18 mg/mm^2 with an average of 0.08 mg/mm^2. Diaspores had between one and eight leaves, but five leaves on average. Fruits per diaspore varied between zero to six fruits with an average of two fruits per diaspore. Galls were found on 53% of the trees, namely on most of the sampled trees from Levka Ori (70%), several from Dikti (30%) but none from Psiloritis (0%). The number of galls varied between 0 and 13, but the average for galled diaspores was three galls per diaspore.

3.2. Variation among trees and mountains of diaspore traits

All of the diaspore traits showed significant ($p < 0.05$) variation amongst trees. In contrast, between mountain ranges, significant variation was found only for diaspore stem length and proportion of fruits with sound seeds per diaspore (Table 2). Diaspores from trees in the Levka Ori had in general higher sound seed proportions and longer diaspore stem lengths than trees from Psiloritis or Dikti, while the latter two had similar values (Table 3). The nested linear models confirmed these findings (Table 4). Indeed, for all diaspore variables except for proportion of fruits with sound seeds per diaspore and diaspore stem length, most of the observed variation found within the variables was imputable to differences amongst trees and not to differences between mountain ranges. Indeed, for most traits the variance for mountain ranges was very low or close to zero. Only diaspore stem length showed slightly higher variation amongst mountain ranges than amongst trees whereas proportion of fruits with sound seeds per diaspore showed over 3.5 times more variation amongst mountain ranges than amongst trees (Table 4).

Table 2

Results of the Kruskal-Wallis rank sum test to test for significance of differences between different trees or mountain ranges for each diaspore trait, fruit weight, proportion of fruits with sound seeds and tree size. Significant ($p < 0.05$) values are given in bold. Degrees of freedom for trees is 35 (except for weight of sound fruits, df: 23) and for mountains is 2 (except for weight of sound fruits, df: 1). NA values are given for variables for which only one value is measured per tree.

Trait	Trees		Mountains	
	X^2	p-value	X^2	p-value
Nb. fruits	300.7	**<0.0001**	0.67	0.72
Nb. leaves	184.15	**<0.0001**	0.62	0.73
Leaf length	294.27	**<0.0001**	0.89	0.64
Leaf width	251.07	**<0.0001**	0.88	0.64
LMA	1075.7	**<0.0001**	3.11	0.21
Stem length	323.14	**<0.0001**	11.88	**0.003**
Nb. galls	363.21	**<0.0001**	5.98	0.05
Prop. sound fr. per diaspore	224.32	**<0.0001**	18.02	**0.0001**
Weight sound fruits	494.53	**<0.0001**	2.14	0.14
Weight unsound fruits	1029.9	**<0.0001**	4.01	0.13
Prop. sound fr. per tree	NA	NA	20.78	**<0.0001**
Tree height	NA	NA	10.31	**0.006**
Trunk circumference	NA	NA	1.26	0.53
Canopy extension	NA	NA	5.06	0.08

Table 3

P-values of pairwise comparisons between mountain ranges using Wilcoxon rank sum test with continuity correction for proportion of fruits with sound seeds per diaspore and per tree as well as diaspore stem length. Significant ($p < 0.05$) values are in bold.

		Psiloritis	Dikti
Prop. sound fruits per diaspore	Levka Ori	**0.03**	**0.0005**
	Psiloritis	–	0.72
Stem length	Levka Ori	**0.002**	**0.04**
	Psiloritis	–	0.08
Prop. sound fruits per tree	Levka Ori	**0.02**	**0.0002**
	Psiloritis	**-**	0.50
Tree height	Lekva Ori	**0.02**	**0.04**
	Psiloritis	**-**	0.11

3.3. Seed soundness per tree

26% of all collected fruits were estimated to have sound seeds. However, seed soundness per tree strongly varied amongst trees, with 32% of investigated trees having 0% of fruits with sound seeds and the remaining 68% of trees having values ranging from 0.15% to 56% of sound seeds (average 23%, Table 5 & Supplementary Material Fig. S3). Seed soundness proportion per tree and proportion of trees with sound seeds strongly varied between regions. In western Crete in the Levka Ori, average seed soundness per tree was 23.59%, and all but one of the sampled trees had fruits with sound seeds. None of the sampled trees of central Crete (Psiloritis) had fruits with sound seeds. In eastern Crete on Mt. Dikti, average seed soundness per tree was 0.64% and only two trees had fruits with sound seeds. Variations in the proportion of seed soundness were significantly different between the three investigated mountain ranges (Table 2), and the Levka Ori had significantly higher sound seed proportions than Psiloritis and Dikti. At the same time, the latter two showed no significant differences (Table 3).

3.4. Fruit weight

Fruit weight was on average 15.45 ± 2.87 mg (range: 11.06–22.17 mg) for sound fruits and 9.12 ± 1.34 mg (range: 5.91–12.95 mg) for

Table 4
Summary of the nested linear models. Two ecological scales were used: trees and mountains. Trees were considered as being nested amongst mountains. The evaluated variables were: leaf width, leaf length, leaf mass per area, diaspore stem length, number of leaves, number of fruits, number of galls, the proportion of fruits with sound seeds per diaspore and fruit weight. Degrees of freedom of trees: 36 (except for sound fruit weight: 24), mountains: 3 (except for sound fruit weight: 2). Variance, standard deviation (Std. dev.) and the number of observations (N) are given.

		Variance	Std. dev.	N
Leaf width	Tree	1.60	1.23	2170
	Mountain	0.00	0.00	
	Residual	5.51	2.35	
Leaf length	Tree	6.95	2.64	2225
	Mountain	0.00	0.00	
	Residual	12.40	3.92	
Leaf mass per area	Tree	0.0002	0.02	2037
	Mountain	0.00003	0.01	
	Residual	0.0002	0.02	
Stem length	Tree	30.39	5.51	534
	Mountain	30.67	5.54	
	Residual	30.39	5.51	
Nb leaves	Tree	0.01	0.11	539
	Mountain	0.00	0.00	
	Residual	1.00	1.00	
Nb fruits	Tree	0.15	0.38	539
	Mountain	0.00	0.00	
	Residual	1.00	1.00	
Nb galls	Tree	7.27	2.70	539
	Mountain	1.24	1.11	
	Residual	1.00	1.00	
Prop. sound fr. per diaspore	Tree	1.81	1.35	501
	Mountain	6.48	2.55	
	Residual	1.00	1.00	
Weight sound fruits	Tree	11.57	3.40	924
	Mountain	1.67	1.29	
	Residual	11.69	3.42	
Weight unsound fruits	Tree	3.59	1.89	1591
	Mountain	0.21	0.46	
	Residual	2.37	1.54	

unsound fruits (Table 5 and Supplementary Material Fig. S4). Wilcoxon signed rank test (on the 24 trees for which there are both sound and unsound fruit weight data) showed that the weight of sound and unsound fruits in a given tree was significantly (p-value <0.001) different. Fruit weight (both sound and unsound) was not found to be significantly different (p-values >0.05) between mountain ranges (Table 2), although sound fruits from Dikti (12.51 mg) were on average lighter than those of Levka Ori (15.71) and the unsound fruits from Psiloritis were on average lighter (7.09 mg) than those of Levka Ori (9.40 mg) and Dikti (9.04 mg), respectively (Table 5). Indeed, fruit weight showed higher variability between trees than amongst mountain ranges (Table 4).

3.5. *Tree size*

Tree height, trunk circumference at breast height and canopy extension for every sampled tree are shown in Table 6 and per mountain range in Supplementary Material Fig. S5. Tree height varied significantly between mountain ranges (Table 2) and was significantly higher in the Levka Ori compared to both Psiloritis and Dikti (Table 3). Psiloritis had the smallest sampled trees, but no statistically significant difference was found with trees from Dikti. Trunk circumference was rather homogenous between mountain ranges and no significant differences were found (Table 2). Although no significant differences were detected between mountain ranges for canopy extension (Table 2), several trees in the Levka Ori had larger canopies than trees anywhere else (Table 6 and Supplementary Material Fig. S5).

3.6. *Correlation between variables*

Spearman's correlation coefficients between diaspore traits, fruit weight, seed soundness and tree size are presented in Fig. 4. The number of fruits per diaspore is significantly positively correlated with LMA and sound fruit weight and is negatively correlated with number of galls per diaspore. In addition, trees that have heavier fruits also tend to have significantly more fruits and leaves per diaspore, bigger leaves, and longer diaspore stems. Fruit weight is not significantly correlated with the proportion of fruits containing sound seeds per diaspore but is positively correlated with the proportion of fruits containing sound seeds per tree. There is no significant correlation between the number of galls and the proportion of fruits with sound seeds. However, a significant negative correlation exists between the number of galls per diaspore and sound fruit weight. In general, the number of galls per diaspore is (significantly or not) negatively correlated with most other variables. In addition, both tree height and canopy extension are significantly and positively correlated with diaspore stem length and proportion of fruits with sound seeds per tree.

4. Discussion

4.1. *Architecture and effectiveness of the diaspores*

Several traits of the diaspores of *Z. abelicea* were analysed for the first time within this study. To our knowledge, only Certini et al. (2020) and Jasińska et al. (2021) mentioned some characteristics of *Z. abelicea* diaspores. Certini et al. (2020) reported (albeit from a single cultivated *Z. abelicea* specimen growing in Switzerland) on average 3.88 leaves (range: 3–6) and 2.00 fruits (range: 1–3) per diaspore. In our study, we found an average of 4.57 leaves (range 1–8) and 1.79 fruits (range 0–6) per diaspore. Since only a single (cultivated) tree was sampled by Certini et al. (2020), we cannot assess if the differences in fruit and leaf number compared to the present study are due to tree specificities or can be imputed to differences in environmental conditions. Jasińska et al. (2021) found averages of 19.80 mm in length and 12.20 mm in width of leaves from fructifying shoots (i.e., diaspores) of *Z. abelicea*. In our study, the average leaf length was 15.56 mm and width 9.10 mm. The slight differences in leaf size found by these authors compared to the values of the current study are probably imputable to differences in sampling strategy, sampling sites and trees as well as sample size. Jasińska et al. (2015, 2021) further studied leaf length and width on fructifying shoots of *Z. carpinifolia* (average 34.3 and 18.2 mm, respectively) and *Z. sicula* (23.9 and 14.0 mm, respectively). These results show that diaspores of *Z. abelicea* have smaller leaves than both other species, measuring half the size of those of *Z. carpinifolia* and about two-thirds the size of the leaves of its Sicilian relative. Moreover, Hoshino (1990) investigated the number of leaves, the number of fruits and the stem length of diaspores of *Z. serrata* individuals from Japan. He found the following average values: 4.10 leaves and 2.70 fruits per diaspore, with an average length of 47.8 mm. Diaspores of *Z. abelicea* have on average more leaves, but fewer fruits and measure ca. half of the length of those of *Z. serrata*.

The short diaspores and small sized leaves of *Z. abelicea* are probably evolutionary adaptations to local conditions and a consequence of the long isolation of the species within its current refugial area, as previously hypothesised by Christe et al. (2014), Garfì et al. (2021) and Jasińska et al. (2021). Indeed, thermo-hydric stress is known to reduce growth in trees (Bréda et al., 2006; Fotelli et al., 2000; Garfì et al., 2021), and plants growing in xeric environments are known to have small leaves that are better adapted to withstand drought than larger ones (Farooq et al., 2009). Wang et al. (2001) state that the small-sized leaves of both Mediterranean *Zelkova* species can be explained by the high levels of evapotranspiration experienced by these species in their habitat during summer.

Z. abelicea has more leaves per diaspore while having shorter stem lengths than *Z. serrata* which implies that the leaves are more densely

Table 5

Total collected fruit counts, number of fruits with sound and unsound seeds, estimated proportion of fruits with sound seeds over the entire seed lot (Est. sound fr. prop) and average weight for sound and unsound fruits. For sound and unsound fruits, the percentage of misplaced fruits (i.e. unsound in sound and vice-versa) is given in parenthesis. Standard deviations of fruit weight per tree are also provided. * shows trees for which the percentage of misplaced fruits was not calculated when there was less than 50 sound fruits.

Mountain	Tree ID	Fruit number			Est. sound fr. prop. (%)	Av. fruit weight (Mg)	
		Total	Sound	Unsound		Sound	Unsound
Levka Ori	XYLO1	1312	297 (2%)	1015 (3%)	22.64	21.77 ± 4.04	12.95 ± 2.23
	CROS1	250	49*	201 (2%)	19.60	11.06 ± 2.94	5.91 ± 1.07
	CROS2	2619	499 (9%)	2120 (0%)	19.05	14.60 ± 1.95	7.35 ± 1.00
	CROS3	3057	634 (0%)	2423 (3%)	20.74	20.52 ± 4.10	12.24 ± 2.47
	XERO1	1175	400 (0%)	775 (4%)	34.04	18.36 ± 3.24	9.34 ± 1.56
	XERO2	5796	2669 (21%)	3127 (9%)	46.05	16.20 ± 2.59	10.39 ± 1.74
	XERO3	923	514 (10%)	409 (3%)	55.69	14.10 ± 2.06	8.90 ± 1.07
	XERO4	12287	6912 (1%)	5375 (13%)	56.25	13.41 ± 2.55	9.72 ± 1.30
	XERO5	5440	2909 (10%)	2531 (0%)	53.47	17.85 ± 6.31	11.08 ± 3.05
	MACH1	2007	637 (0%)	1370 (0%)	31.74	22.17 ± 3.74	10.44 ± 1.84
	MACH2	2055	857 (0%)	1198 (0%)	41.70	19.44 ± 3.22	11.22 ± 1.17
	MACH3	2056	1003 (10%)	1053 (6%)	48.78	20.45 ± 2.85	12.24 ± 1.61
	LOFO1	873	132 (3%)	741 (10%)	15.12	15.28 ± 3.02	10.05 ± 1.46
	LOFO2	840	177 (3%)	663 (6%)	21.07	13.78 ± 2.88	8.78 ± 1.62
	LOFO3	1347	186 (8%)	1161 (2%)	13.81	13.74 ± 2.33	8.13 ± 1.36
	THER1	1470	231 (2%)	1239 (0%)	15.71	17.43 ± 3.14	11.49 ± 1.54
	THER2	388	76 (3%)	312 (13%)	19.59	12.70 ± 2.97	8.93 ± 1.76
	THER3	2368	285 (17%)	2083 (3%)	12.04	11.88 ± 2.05	6.21 ± 1.14
	THER4	1062	197 (2%)	865 (7%)	18.55	11.23 ± 1.47	6.63 ± 0.82
	IMB1	1340	4*	1336 (0%)	0.30	13.75 ± 3.18	8.63 ± 0.79
	IMB2	1317	2*	1315 (0%)	0.15	NA	6.52 ± 0.81
	IMB3	2221	30*	2191 (0%)	1.35	11.71 ± 1.34	7.42 ± 0.88
	IMB4	1403	15*	1388 (0%)	1.07	14.28 ± 2.62	9.56 ± 0.96
	VILL1	429	0	429 (0%)	0.00	–	11.55 ± 1.27
Psiloritis	PSI1	49	0	49 (0%)	0.00	–	7.60 ± 0.94
	PSI2	34	0	34 (0%)	0.00	–	6.56 ± 1.40
	PSI14	78	0	78 (0%)	0.00	–	7.12 ± 1.10
Dikti	PROT1	4426	0	4426 (0%)	0.00	–	8.82 ± 1.04
	PROT2	3063	0	3063 (0%)	0.00	–	9.62 ± 1.22
	PROT3	5696	0	5696 (0%)	0.00	–	9.57 ± 1.10
	VIAN1	623	0	623 (0%)	0.00	–	8.00 ± 1.11
	VIAN2	1467	0	1467 (0%)	0.00	–	8.06 ± 1.32
	LAS1	951	0	951 (0%)	0.00	–	9.37 ± 1.17
	LAS2	786	0	786 (0%)	0.00	–	9.93 ± 0.95
	LAS3	935	0	935 (0%)	0.00	–	12.69 ± 1.81
	KATH1	721	13*	708 (0%)	1.80	13.26 ± 2.27	7.41 ± 0.94
	KATH2	153	7*	146 (0%)	4.58	11.77 ± 2.11	6.94 ± 0.86
	Total	73017	18735 (6%)	54282 (3%)	15.54	15.45 ± 2.87	9.12 ± 1.34
	Levka Ori (N = 24)	54035	18715	35320	23.69	15.71 ± 2.94	9.40 ± 1.44
	Psiloritis (N = 3)	161	0	161	0	–	7.09 ± 1.15
	Dikti (N = 10)	18821	20	18801	0.64	12.51 ± 2.19	9.04 ± 1.15

arranged on the diaspore. Despite these structural differences, Certini et al. (2020) pointed out that flight mechanisms and velocity of diaspores were similar in both species, suggesting a remarkable evolutionary conservation of the traits responsible for dispersal. We hypothesise that leaf blade size reduction – most likely an adaptive trait related to more xeric environmental conditions as discussed above – is compensated by an increase in the number of leaves to preserve flight and dispersal effectiveness. However, this topic, as well as the fact that *Z. abelicea* has fewer fruits per diaspore compared to its Asian relative, need yet to be further investigated.

4.2. Fruit weight

Until the present study, the only published records concerning fruit weight in *Z. abelicea* were those reported by Fournaraki and Thanos (2002) and Certini et al. (2020). The former reported an average weight of 15.22 ± 0.22 mg for 120 sound fruits collected from a single location (unknown number of trees) in the Omalos region in the Levka Ori mountains in western Crete. Fournaraki and Thanos (2002) also stated that fruits with unsound seeds usually weigh less than 10 mg but did not give more details, nor how many fruits they weighed. Certini et al. (2020) sampled a single cultivated tree growing in Switzerland, which had only fruits with unsound seeds and gave an average weight of 10.6 mg (27 fruits, range 8–13 mg). With the present study, we analysed the fruit weight of 2519 fruits (1591 unsound, 928 sound) from throughout the distribution range of *Z. abelicea*. The among-tree average of 15.45 mg for sound fruits is similar, albeit slightly higher than the above-mentioned value found by Fournaraki and Thanos (2002). For unsound fruits, we found lower values than those given by Certini et al. (2020). Moreover, in our study, we noticed that fruit weight is highly fluctuant amongst trees (Table 5) and that no significant differences were found between mountain ranges. Indeed, trees taken in the same area as Fournaraki and Thanos (2002) and less than 4 km apart from one another hold the average maximum (22.17 mg, MACH1) and minimum (11.06 mg, CROS1) fruit weight for sound fruits and also maximum (12.95 mg, XYLO1) and minimum (5.91 mg, CROS1) fruit weight for unsound fruits. Nevertheless, sound fruits of trees from the Levka Ori are on average heavier than those from Dikti (but the very small sound fruit sample size of Dikti may have biased the results), whereas unsound fruits from Psiloritis are lighter than those of the two other mountain ranges.

Table 6
Tree size variables: tree height, trunk circumference (circum) at breast height and canopy extension (can. ext.) for each sampled tree with mountain-wise averages.

Mountain	Tree ID	Height (m)	Circum (m)	Can. ext. (m)
Levka Ori	XYLO1	10.93	1.44	20.70
	CROS1	8.27	0.63	12.00
	CROS2	11.85	0.55	9.50
	CROS3	5.36	0.66	12.10
	XERO1	7.30	0.70	16.50
	XERO2	12.61	2.75	21.00
	XERO3	11.58	1.76	25.20
	XERO4	7.09	0.83	11.80
	XERO5	9.09	0.84	17.20
	MACH1	9.35	0.82	11.40
	MACH2	14.04	2.21	20.40
	MACH3	9.64	1.44	19.80
	LOFO1	6.13	0.60	9.90
	LOFO2	8.77	0.41	5.40
	LOFO3	9.89	0.94	15.80
	THER1	8.41	0.70	12.60
	THER2	8.23	1.06	13.90
	THER3	11.41	1.15	13.10
	THER4	7.01	0.90	13.10
	IMB1	10.52	1.25	17.80
	IMB2	14.28	1.20	17.90
	IMB3	11.29	1.27	20.10
	IMB4	8.10	1.37	19.60
	VILL1	3.50	0.40	4.65
Mountain average		9.36	1.08	15.06
Psiloritis	PSI1	4.81	1.40	11.80
	PSI2	3.55	0.80	11.70
	PSI14	6.01	0.95	12.80
Mountain average		4.79	1.05	12.10
Dikti	PROT1	8.34	2.30	16.40
	PROT2	8.31	0.86	NA
	PROT3	8.73	1.90	9.70
	VIAN1	6.51	0.75	13.10
	VIAN2	8.01	0.82	12.80
	LAS1	5.54	0.50	7.60
	LAS2	3.91	0.36	6.20
	LAS3	5.45	0.68	12.00
	KATH1	5.94	0.50	10.40
	KATH2	10.16	0.94	12.70
Mountain average		7.09	0.96	11.21

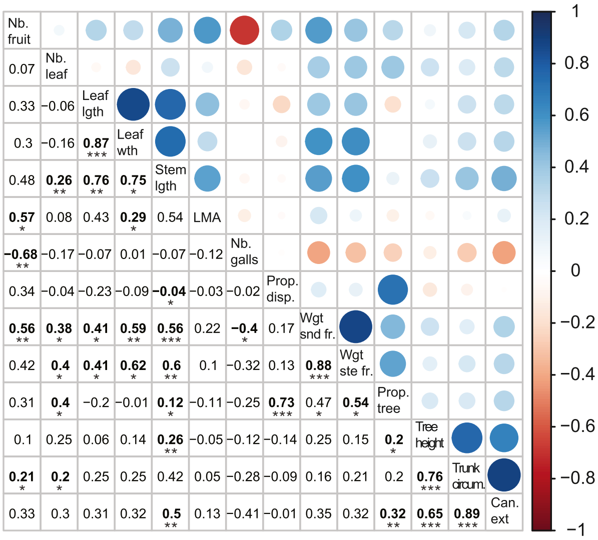

Fig. 4. Spearman's rank correlation results between diaspore traits, fruit weight, proportion of fruits with sound seeds per tree and tree size. Leaf lgth: leaf length, leaf wth: leaf width, stem lgth: diaspore stem length, LMA: leaf mass per area, prop. disp.: proportion of fruits with sound seeds per diaspore, wgt snd fr.: weight sound fruits, wgt ste fr.: weight unsound fruits, prop. tree: proportion of fruits with sound seeds per tree, trunk circum: trunk circumference, can. ext.: canopy extension. Significant rho estimates are given in bold with significance levels (*p < 0.05, **p < 0.01, ***p < 0.001). Red circles indicate negative correlations while blue circles indicate positive correlations.

4.3. Seed soundness within diaspores and trees: a longitude-dependent fitness pattern

Twenty-five out of the thirty-seven sampled trees (i.e., 68%) had fruits with sound seeds, with a vast soundness variation ranging from 0.15% to 56.25%. These values are in line with the few and geographically restricted previous studies (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007). The positive correlation between seed soundness rates of trees and diaspores shows that in general, trees that have higher proportions of sound fruits also have higher ratios of sound fruits per diaspore.

A highly interesting finding is the striking geographical difference in seed soundness. Indeed, all but one sampled tree from Levka Ori had fruits with sound seeds, whereas soundness reached only 20% in Dikti and was null for all sampled trees from Psiloritis. This means that based on our study, for a majority of trees growing in the populations located outside of the westernmost mountains (Levka Ori), the production of sound seeds is relatively poor. These results suggest that seed soundness is most probably strongly influenced by a factor following a longitudinal gradient in Crete. Such an assumption goes in the same direction as the findings of Fazan et al. (2022a) who found that shoots of Z. abelicea trees in western Crete grow more than shoots of trees in eastern Crete due to a west-to-east gradient of seasonal precipitation. It is most probable that this climatic gradient also strongly impacts the reproductive biology of the species. At present it is not possible to test this assumption further due to the need for precise enough weather data for interpolating weather patterns occurring in the Cretan mountains (see Fazan et al., 2022a for a discussion on the subject). Further research should be carried out to understand why embryos do not develop in some seeds, and if this could be due to a pollination failure, or if embryos started developing and then halted due to, e.g., embryo development limiting environmental conditions.

In addition, we lack a multi-year perspective to see if our results could differ depending on yearly precipitation amounts and/or in relation to masting events. Other authors have shown that fruit weight tends to be stable for a given tree species between years (Augspurger et al., 2016). Water stress, however, has been found to explain higher levels of seed abortion in other Mediterranean tree species (e.g., Espelta et al., 2008; García et al., 2000; Pérez-Ramos et al., 2010). The fact that the proportion of sound seeds is deficient in central and eastern Crete, coupled with less favourable growth conditions, could explain the absence of *Z. abelicea* seedlings already recorded by Fazan et al. (2021) in those areas. The fact that all sampled trees in Psiloritis had unsound seeds, while at the same time having the lowest fruit weight is preoccupying. These results may be biased by the small sample size in that location, but could also mirror more adverse conditions, inhibiting normal seed and fruit development. Indeed, Fazan et al. (2022b) also showed poorer site conditions in Psiloritis than other sites hosting *Z. abelicea* trees. Nevertheless, since Christe et al. (2014) found strong genetic differences in *Z. abelicea* populations growing on each mountain range, we cannot rule out a possible genetic control that would be mirroring the longitudinal gradient found in terms of diaspore stem length and proportion of fruits with sound seeds.

4.4. The importance of intraspecific trait variations

Most of the investigated traits showed stronger between-tree variation than between-mountain variation. This result supports the highly conservative aspect of the investigated traits within the species, despite a history of mountainwise isolation and drift (Christe et al., 2014).

Moreover, this also suggests the absence of a significant influence of environmental factors on many traits. High intraspecific variation in traits linked with dispersal is not uncommon in tree species (e.g. Augspurger et al., 2016; Sipe and Linnerooth, 1995; Song et al., 2020; Wyse et al., 2019) and may result from high heritability (Wyse et al., 2019). However, it could also be a kind of bet-hedging strategy (Song et al., 2020; Wyse et al., 2019), to maximise the species chances of effective dispersal and may have important evolutionary and ecological implications (Sipe and Linnerooth 1995). In addition, in a context of rapidly changing climatic conditions, high intraspecific variation may also benefit to the species (Chevin et al., 2010; Forsman, 2013).

4.5. Influence of tree size and galls on seed soundness

Our results showed a positive relationship between larger tree size, higher proportion of sound seeds per tree, heavier fruit weight and longer diaspores with more fruits and leaves. Sampled trees from Levka Ori were also bigger, although not significantly, than those from Psiloritis and Dikti. These findings, in addition to the mountain-wise difference in proportion of fruits with sound seeds tend to point towards a general reduction trend outside of the Levka Ori, both in terms of number and size of diaspore traits but also tree size. Reduction patterns and small size are considered an adaptive response to thermo-hydric stress (Abeli et al., 2014; Garfì et al., 2002, 2021). These assumptions are supported by the strong climatic gradients found on Crete, with a sharp decrease in precipitation occurring from west to east (Agou et al., 2019; Goedecke and Bergmeier, 2018; Varouchakis et al., 2018). In addition, an increase in LMA is visible eastwards (Supplementary Material, Fig. S2E), although differences between mountain ranges are not significant. LMA has been reported to be negatively correlated with soil water content and availability as it increases with water stress (de la Riva et al., 2016; Poorter et al., 2009), therefore clearly demonstrating that trees in central and eastern Crete suffer more from water depletion than trees in western Crete.

A biotic agent was also found to affect fruit production and negatively correlate with most tree traits. Galls were found on 53% of the sampled trees. However, this result strongly depended on the sampling design, and numbers may have been entirely different if other trees had been sampled. The number of galls per diaspore does not seem to follow a geographical pattern on the island but varies according to the sampled tree. Galls were present or absent from some trees both in western and eastern Crete, although none of the investigated trees in Psiloritis contained galls, suggesting unsuitable conditions for the development of the Cecidomyiidae larvae or an absence of colonisation by the insect in this area. No strong and significant relationship between seed soundness and gall presence or quantities were found, which reinforces the idea that seed soundness is mainly driven by environmental gradients. Nevertheless, we found a clear trend showing that diaspores with higher number of galls tended to have fewer and lighter fruits, and galls were overly negatively correlated, albeit often not significantly, with most other variables. Although further investigations should be carried out, this could imply a negative effect of gall abundance and presence on flowering or fruit production. This could be explained by the fact that the larvae cause abnormal development and functioning of stamens, therefore, preventing pollination, or that plants invest energy to produce galls, thus inducing a shortage of resources to be allocated to viable embryo development (Collins and Drummond, 2019; Koprdova et al., 2015).

4.6. Implications for conservation

Our findings suggest that morphological traits of diaspores are ultimately not significantly affecting the functioning of dispersal mechanisms of *Z. abelicea* at an inter-population level. This is not the case for recruitment through seed, which is relatively successful in the westernmost populations but is entirely ineffective in those from central and eastern Crete. In these latter areas, *Z. abelicea* trees produce lower to null sound fruit proportions, are smaller and their diaspores and fruit weight show features typical of trees suffering (more) from suboptimal growth conditions compared to those of western Crete. This fact is alarming for the long-term persistency of *Z. abelicea*, at least outside of the Levka Ori mountain range. Although *Z. abelicea* is known to sucker profusely, especially after disturbance events (Egli, 1997; Fazan et al., 2012; Kozlowski et al., 2018), the absence of sexual reproduction and/or efficient recruitment will ultimately lead to the reduction or even to the disappearance of the most marginal populations (García et al., 2000; Hampe, 2005; Hampe and Arroyo, 2002). The fact that no fruiting trees were observed in the easternmost population of Thripti may already point towards this ongoing process. The lack of sexual reproduction and the shrinkage or extinction of *Z. abelicea* populations on a local scale will impoverish the high genetic diversity still detected within the species (Christe et al., 2014) and thus impact the evolutionary and adaptation potential to climate change of the remnant populations (Hampe and Petit, 2005).

5. Conclusions

Diaspore traits, fruit weight and seed soundness of *Z. abelicea* were studied for the first time over the whole species distribution range. We found substantial variability between trees but less so between mountain ranges. However, the few variables that varied depending on the mountain range all point towards trees thriving better in western Crete. Seed soundness showed a clear longitudinal pattern, probably following a gradient in environmental factors, the most probable being longitudinal precipitation gradients. Trees in central and eastern Crete seem to suffer more from water-limiting climatic conditions than trees in western Crete. These findings are preoccupying for the long-term persistency of *Z. abelicea* in the most marginal parts of its natural distribution range.

Author contributions

Laurence Fazan: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing – Original Draft, Visualization, Project administration, **Daniele Certini**: Writing – Review & Editing, **Salvatore Pasta**: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing – Review & Editing, **Ilektra Remoundou**: Writing – Review & Editing, **Dany Ghosn**: Writing – Review & Editing, **Giuseppe Garfì**: Conceptualization, Methodology, Investigation, Writing – Review & Editing, Supervision, **Gregor Kozlowski**: Writing – Review & Editing, Supervision, Project administration, Funding acquisition.

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Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2023.103896.

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Supplementary material

Table S1. Latitude (DD), longitude (DD) and altitude (m a.s.l.) of each sampled tree. The number of weighted fruits per tree according to seed soundness (sound or unsound) are also given.

				Number	
Tree ID	Latitude	Longitude	Altitude	Sound	Unsound
XYLO1	35.31	23.91	1217	52	31
CROS1	35.32	23.91	1128	18	56
CROS2	35.32	23.91	1130	30	33
CROS3	35.32	23.91	1119	54	30
XERO1	35.32	23.91	1158	52	48
XERO2	35.31	23.90	1202	37	48
XERO3	35.31	23.90	1199	28	32
XERO4	35.31	23.90	1240	85	28
XERO5	35.31	23.90	1241	93	126
MACH1	35.32	23.92	1178	50	50
MACH2	35.32	23.92	1195	30	30
MACH3	35.32	23.92	1218	49	53
LOFO1	35.34	23.91	1068	32	28
LOFO2	35.34	23.91	1067	31	30
LOFO3	35.34	23.91	1099	47	53
THER1	35.38	23.99	988	45	37
THER2	35.38	23.99	1077	39	29
THER3	35.38	23.99	1130	66	42
THER4	35.38	23.99	1131	47	29
IMB1	35.27	24.15	1161	4	52
IMB2	35.27	24.15	1156	2	51
IMB3	35.27	24.15	1191	14	56
IMB4	35.27	24.15	1176	8	50
VILL1	35.25	24.18	813	0	51
PSI1	35.18	24.93	1322	0	13
PSI2	35.18	24.93	1337	0	20
PSI14	35.18	24.93	1323	0	10
PROT1	35.07	25.51	1644	0	50
PROT2	35.07	25.51	1635	0	50
PROT3	35.07	25.51	1613	0	50
VIAN1	35.06	25.47	1138	0	50
VIAN2	35.06	25.47	1321	0	50
LAS1	35.17	25.54	1191	0	30
LAS2	35.17	25.54	1180	0	30
LAS3	35.16	25.54	1174	0	55
KATH1	35.13	25.53	1247	9	55
KATH2	35.14	25.57	1119	6	55
Mean	-	-	-	37	43

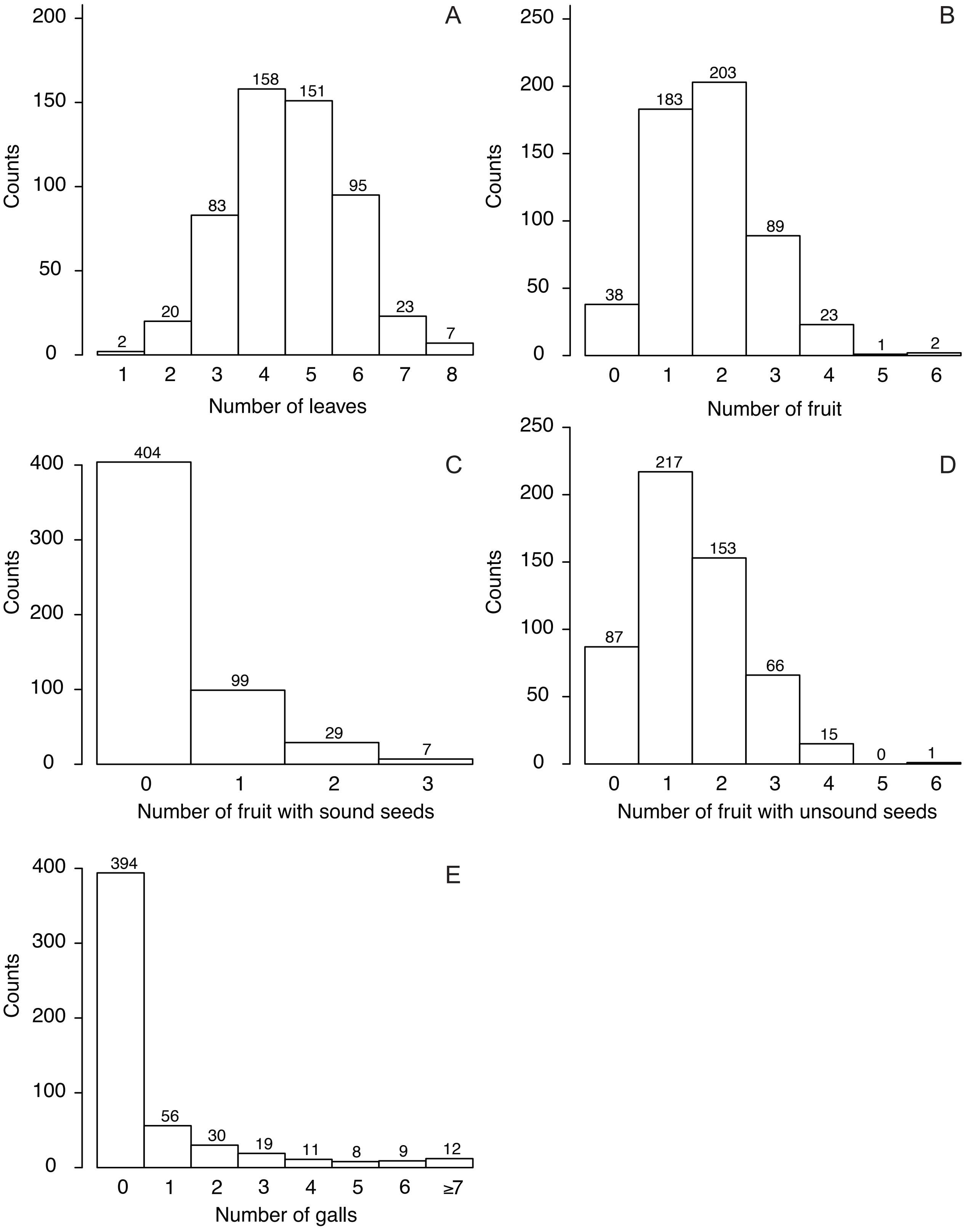

Figure S1. Histograms for discrete diaspore traits. A. number of leaves per diaspore, B, number of fruits per diaspore, C. number of fruits with sound seeds per diaspore, D. number of fruits with unsound seeds per diaspore, E. number of galls per diaspore.

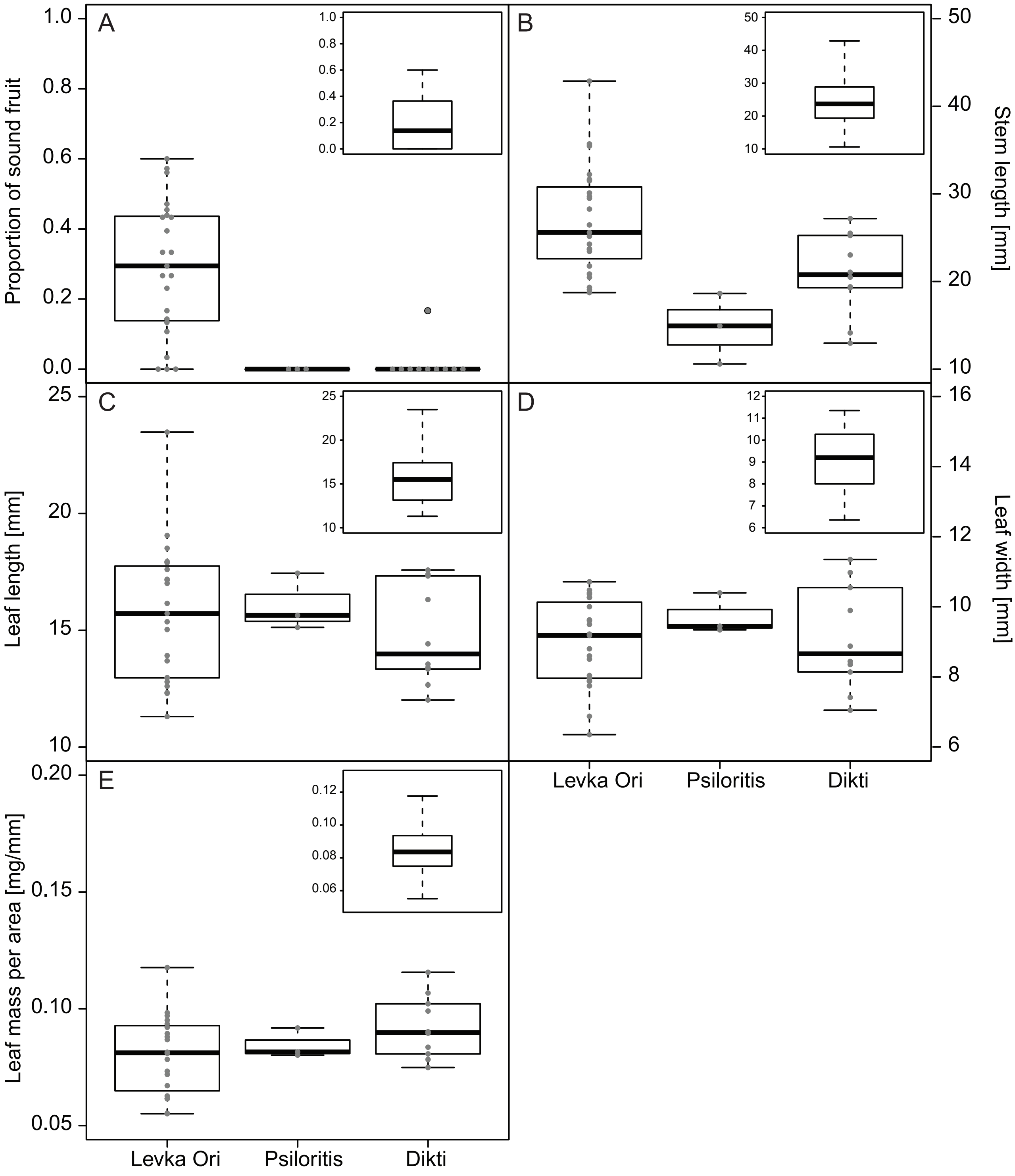

Figure S2. Per tree average diaspore traits for each of the three investigated mountain ranges, from west to east: Levka Ori, Psiloritis, Dikti. A. proportion of fruits with sound seeds per diaspore, B. stem length, C. leaf length, D. leaf width, E. leaf mass per area. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as circles. Grey dots represent individual tree mean values. Miniatures represent overall data.

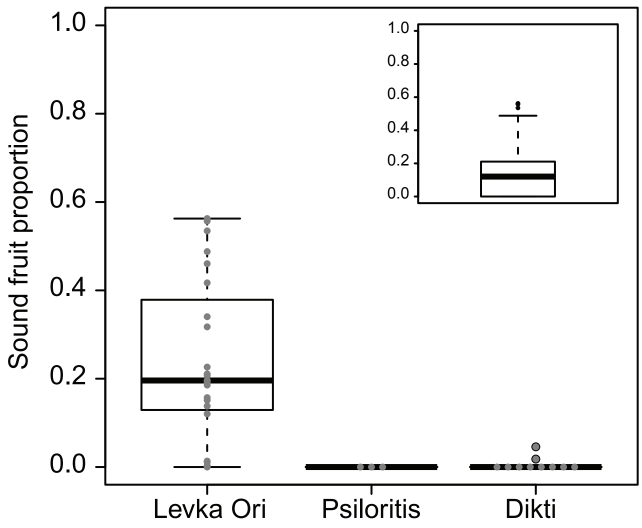

Figure S3. Proportion of fruits with sound seeds per tree for each mountain range. Grey dots represent individual trees. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as circles. Miniatures represent overall data.

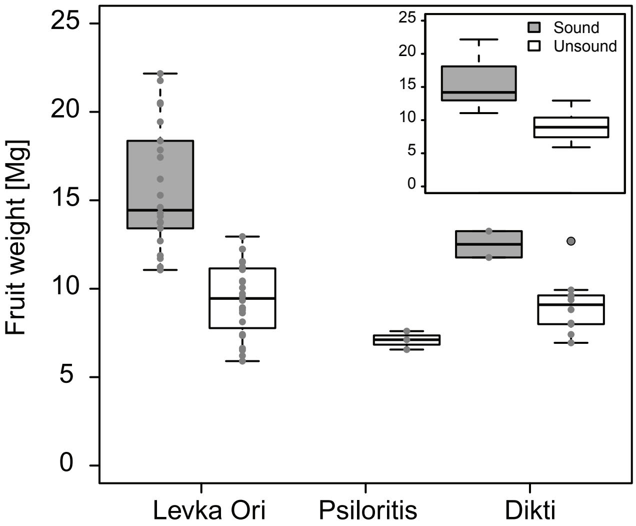

Figure S4. Fruit weight for sound (grey) and unsound (white) fruits for each mountain range. Grey dots represent individual trees. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as circles. Miniatures represent overall data. For Psiloritis, no fruit with sound seeds were found.

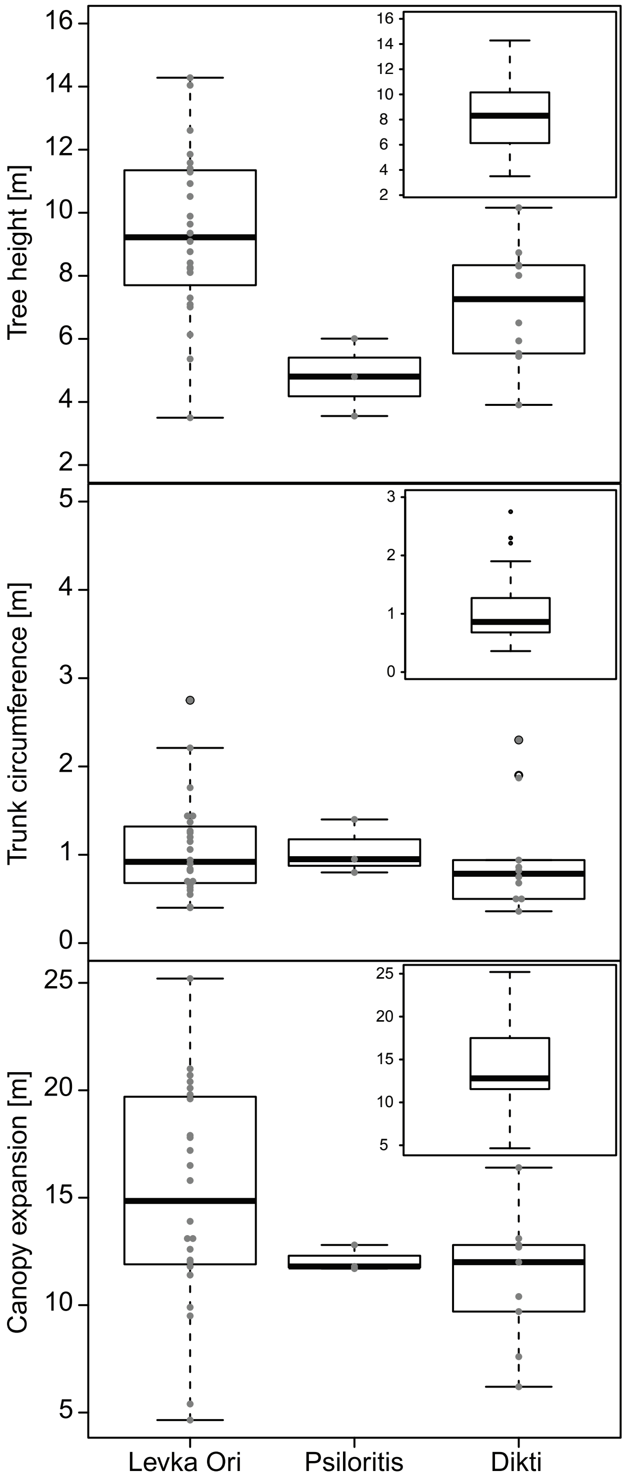

Figure S5. Boxplots representing tree height, trunk circumference and canopy extension for each of the three mountain ranges. Grey dots represent individual trees. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as circles. Miniatures represent overall data.

CHAPTER 4

FACTORS INFLUENCING THE DIVERSITY AND DISTRIBUTION OF EPIPHYTIC LICHENS AND BRYOPHYTES ON THE RELICT TREE *ZELKOVA ABELICEA* (LAM.) BOISS. (ULMACEAE)

Laurence Fazan, Dariusz J. Gwiazdowicz, Yann Fragnière, Wieslaw Faltynowicz, Dany Ghosn, Ilektra Remoundou, Anna Rusinska, Pawel Urbanski, Salvatore Pasta, Giuseppe Garfì, Gregor Kozlowski

Author contributions: LF, DJG and GG conceived the study, DJG, DG, IR collected plant samples, AR and PU identified bryophyte samples, WF identified lichen samples, WF, AR and PU offered taxon specific specialist support, LF and YF performed the statistical analyses, LF wrote the manuscript, LF, DJG, YF, WF, DG, IR, AR, PU, SP, GG and GK reviewed the manuscript.

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Standard Paper

Factors influencing the diversity and distribution of epiphytic lichens and bryophytes on the relict tree *Zelkova abelicea* (Lam.) Boiss. (*Ulmaceae*)

Laurence Fazan[1], Dariusz J. Gwiazdowicz[2], Yann Fragnière[1], Wiesław Fałtynowicz[3], Dany Ghosn[4], Ilektra Remoundou[4], Anna Rusińska[5], Paweł Urbański[6], Salvatore Pasta[7], Giuseppe Garfì[7] and Gregor Kozlowski[1,8,9]

[1]Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland; [2]Poznań University of Life Sciences, Faculty of Forestry, Poznań, Poland; [3]Department of Botany, Wrocław University, Wrocław, Poland; [4]Department of Geoinformation in Environmental Management – CIHEAM Mediterranean Agronomic Institute of Chania, Alsyllio Agrokepiou, 73100 Chania, Greece; [5]Natural History Collections, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland; [6]Department of Botany, Poznań University of Life Sciences, Poznań, Poland; [7]Institute of Biosciences and BioResources – National Research Council, Corso Calatafimi 414, 90129 Palermo, Italy; [8]Natural History Museum Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland and [9]Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, 3888 Chenhua Road, Songjiang, 201602 Shanghai, China

Abstract

Trees have a crucial importance in the functioning of ecosystems on Earth. They are among the largest and longest-living taxa and provide habitat and shelter to numerous species belonging to diverse groups of organisms. Relict trees are of particular interest through their history of survival and adaptation, and because they potentially shelter rare or threatened organisms today. We investigated for the first time the diversity and distribution of epiphytic lichens and bryophytes found on the Cretan (Greek) endemic and relict phorophyte *Zelkova abelicea* (*Ulmaceae*). Our results showed that *Z. abelicea* hosts a high number of epiphytes. The Levka Ori mountain range in western Crete seems to be a hot spot for epiphytic lichens on *Z. abelicea*. Bryophytes had the highest diversity on Mt Kedros in central Crete but were absent from several other sites. Moreover, 17% of the studied lichens were recorded for the first time for Crete and 5% have never been recorded for Greece. Geographical position and browsing intensity seem to be important factors influencing the epiphytic community encountered. Tree morphology (dwarfed or arborescent) was also significant in influencing community composition although it was not possible to dissociate this factor from the effect of topography. Dwarfed individuals were found to have as much epiphytic diversity as arborescent trees. Ecological indicator values showed that high epiphytic diversity was found in some sites despite signs of eutrophication and disturbance due to pastoral activities and suggest the co-occurrence of both disturbance tolerant and sensitive species. Our results show how little is known about the biodiversity of Cretan phorophytes and highlights the need for further research on the topic.

Key words: Crete, dwarfed over-browsed trees, ecological indicator values, epiphytic assemblages, Greece, phorophyte

(Accepted 25 March 2022)

Relict trees are particularly interesting because they have survived and adapted to changing environmental conditions throughout millions of years and are the only representatives of previously widespread taxa (Kozlowski & Gratzfeld 2013; Grandcolas *et al.* 2014). Little research has yet been undertaken to make an inventory of the biodiversity linked specifically with relict trees. However, relict trees have been found to be of crucial importance in maintaining and giving shelter to widespread as well as rare, endemic or other relict taxa. This is the case, for example, with *Zelkova sicula* Di Pasq. *et al.* (Barbagallo 2002; Barbagallo *et al.* 2009) or *Dracaena cinnabari* Balf.f. (Rejžek *et al.* 2016; Maděra *et al.* 2019).

Furthermore, relict tree stands often contain very old trees (Fazan *et al.* 2012; Tang *et al.* 2013; Camarero *et al.* 2018), and old trees are known to provide numerous microhabitats (Lindenmayer & Laurance 2017; Nordén *et al.* 2018). These microhabitats (sometimes denominated in literature as 'tree related microhabitats'; Kraus *et al.* 2016; Larrieu *et al.* 2018; Bütler *et al.* 2020) can also be formed by tree-associated taxa such as bryophytes or lichens. Some in turn foster a wide variety of other living organisms (e.g. invertebrates, plants, fungi, birds) and play a key role in maintaining or even increasing biodiversity (Paillet *et al.* 2010).

The genus *Zelkova* (*Ulmaceae*) is a relict from the so-called Arctotertiary geoflora (Mai 1991) whose members were important

Author for correspondence: Gregor Kozlowski. E-mail: gregor.kozlowski@unifr.ch

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components of forests of the Northern Hemisphere during the Paleogene. Only six extant species of this genus are found today, and they show a remarkable disjunct distribution: *Z. serrata* (Thunb.) Makino, *Z. schneideriana* Hand.-Mazz. and *Z. sinica* Schneid. occur in eastern Asia, *Z. carpinifolia* (Pall.) Koch grows in the Transcaucasian region and Middle East, while *Z. sicula* and *Z. abelicea* (Lam.) Boiss. are endemic to the Mediterranean islands of Sicily (Italy) and Crete (Greece), respectively (Kozlowski & Gratzfeld 2013).

Zelkova abelicea grows in the mountainous regions of Crete above 900 m a.s.l., in rather cool and not too xeric sites such as north-facing slopes or around dolines (sinkholes), or at high elevations on south-facing slopes (Egli 1997; Søndergaard & Egli 2006; Fazan *et al.* 2012; Goedecke & Bergmeier 2018). Due mainly to overbrowsing by goats, most individuals have a stunted dwarfed form, with multiple stems, a shrubby morphology and very slow growth (Fazan *et al.* 2012). Such individuals account for up to 95% of all populations, with some stands composed entirely of dwarfed plants (Kozlowski *et al.* 2014). Dwarfed individuals have been found to reach several hundred years in age and in some cases are older than arborescent trees (Fazan *et al.* 2012). Arborescent, 15–20 m high individuals are much rarer. Old arborescent *Z. abelicea* trees show signs of having been pollarded in the past, and their leaves were used as summer forage (Rackham & Moody 1996; Bauer & Bergmeier 2011). These old trees are often found growing next to abandoned shepherd huts to which they probably provided shade. The recruitment of seedlings is difficult due to the almost permanent overbrowsing during the growing season and dry summer conditions influencing plant growth and seedling establishment (Egli 1997; Søndergaard & Egli 2006; Fazan *et al.* 2012; Kozlowski *et al.* 2014, 2018).

The overall number of lichen and bryophyte species known for Greece is small, despite significant recent progress in the study of both taxonomic groups. The first and only published lichen checklist of Greece (Abbott 2009) recorded almost 1300 species, while the most recent, online checklist (Arcadia 2022) already includes *c.* 1500 taxa. This indicates there is ongoing dedication towards this group of organisms in the region, as supported by the studies in recent years of a dozen lichenologists occasionally working in Greece (Obermayer 1997; Papp *et al.* 1999; Sipman & Raus 1999, 2002; Christensen 2000, 2007, 2014, 2018; Grube *et al.* 2001; Spribille *et al.* 2006; Christensen & Svane 2007; Vondrák *et al.* 2008). Furthermore, although Crete also offers a wide spectrum of habitats, only a small number of lichen species are known from this island (Vondrák *et al.* 2008), only 677 species according to Arcadia (2022).

Several authors have recorded bryophytes in Greece throughout the 20th century (e.g. Coppey 1907, 1909; Preston 1981, 1984; Düll 1995), each time with an increasing number of species. In the 1980s, Preston (1984) reported 424 species, whereas more recent national inventories included 525 moss taxa (Sabovljević *et al.* 2008) or 690 species when considering both mosses (536 spp.) and liverworts (154 spp.; Blockeel 2013). Ros-Espin *et al.* (2013) reported over 590 moss taxa from mainland Greece and slightly over 280 taxa from Crete, of which *c.* 25% have been recorded only once. This again shows how little these groups of organisms have been studied until recently and suggests a need for more detailed investigations of lichens and bryophytes on the island.

Studies including or focusing on the phorophyte species of Crete exist but are rare (e.g. Kleinig 1966; Gradstein 1971; Werner 1998; Grube *et al.* 2001; Spribille *et al.* 2006; Christensen 2007, 2014; Vondrák *et al.* 2008), and none has addressed *Z. abelicea* specifically. The only record of epiphytes growing on *Z. abelicea* comes from Spribille *et al.* (2006), which mentions four macrolichen species that are common for Crete.

In this study, we focus on a so far neglected portion of the biodiversity linked with *Z. abelicea*, by investigating the lichens and bryophytes that use this species as a phorophyte. It is the first time that an attempt to list these groups of organisms has been made by targeting *Z. abelicea* and covering all mountain ranges where the tree species occurs. More specifically, we aimed to answer the following questions: 1) What is the diversity of epiphytic lichens and bryophytes on *Z. abelicea*? 2) Do *Z. abelicea* trees host specific epiphyte taxa that are found nowhere else? 3) What is their distribution on *Z. abelicea* individuals throughout Crete? 4) Which environmental factors might influence the observed epiphytic diversity and community composition? 5) Does one site or another stand out in terms of ecological indicator values?

Methods

Specimen and data collection

Specimens were collected in autumn 2018 and spring 2019 from eight study sites, covering the whole distribution range of *Zelkova abelicea* on Crete (Fig. 1). Three study sites were located in the Levka Ori (Omalos, Niato and Impros), one on Mt Kedros (Gerakari), one on Mt Psiloritis (Rouvas), two in the Dikti Mountains (Viannou and Katharo), and one in the Thripti Mountains (Thripti). In each site, two to seven individuals (dwarfed or arborescent; Fig. 2A & B) of *Z. abelicea* were sampled, giving a total of 36 individuals. In Niato and Thripti, sampling was carried out only on dwarfed trees as no arborescent individuals were present. On non-dwarfed trees, the top layer of bark (Fig. 2C) hosting epiphytes was cut off with a knife, without harming the vital, living parts of the tree trunk. In dwarfed individuals, whole twigs covered with epiphytes were cut off with a knife (Fig. 2D). The collected material was placed in paper bags and kept dry until identification.

In each of the study sites, the following general information was also collected: geographical coordinates (latitude and longitude), altitude, topography (slope or doline floor) and browsing intensity (Table 1).

Gridded climatic data (i.e. annual mean temperature and sum of annual precipitation) for the period 1970–2000 were extracted from WorldClim (www.worldclim.com/version2) at a 30 s (i.e. *c.* 1 km^2) resolution (Fick & Hijmans 2017) for each study site (Table 1).

Species identification

Epiphytic material was determined using standard stereoscopic and light microscopy. The taxonomic identity of the sampled material was assessed using identification keys. Lichens were determined using keys provided by Clauzade & Roux (1985), Smith *et al.* (2009) and Arcadia (2022). In a small number of necessary cases, thin-layer chromatography was used. Nomenclature of lichen species followed Index Fungorum (Index Fungorum Partnership 2022). Information on the morphological type of thallus (Cr – crustose, Fo – foliose, Fr – fruticose; Fig. 2E–G) was obtained from Arcadia (2022).

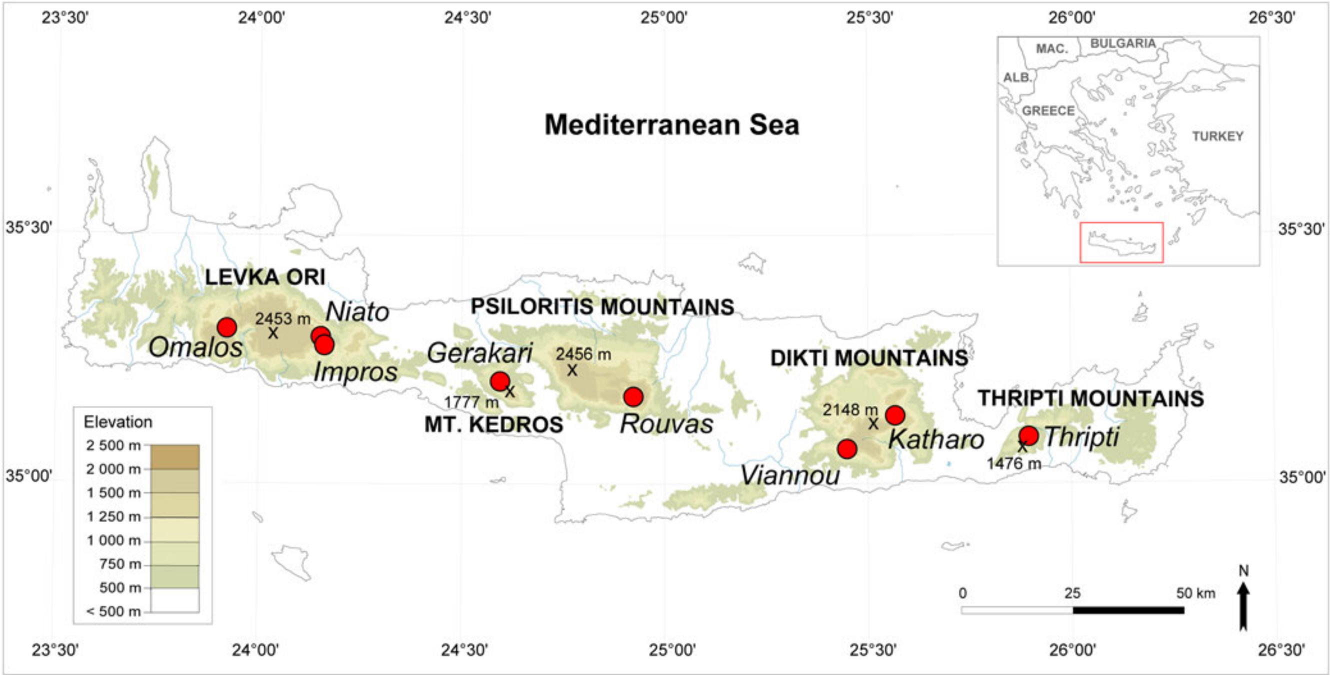

Fig. 1. Location of the eight study sites (filled dots) distributed across all five Cretan mountain ranges that contain populations of *Zelkova abelicea*. Names in bold font indicate mountain ranges with stands of *Z. abelicea*; summits (m) are indicated with an 'X'. The names of the study sites are given in italic font. In colour online.

Bryophytes were determined using the keys provided by Nyholm (1965, 1998), Smith (1978) and Ros-Espin *et al.* (2013). Nomenclature of bryophytes followed Ros-Espin *et al.* (2013). For each bryophyte taxon, the morphological type (P – pleurocarpous, A – acrocarpous) was obtained from Düll (1979) and Preston (1984).

Authorities for cited lichen and bryophyte species are given in Tables 2 & 3. The analyzed material was deposited in the collections of the University of Wrocław, Poland (lichens) and in the Natural History Collections of Adam Mickiewicz University in Poznań, Poland (bryophytes).

Statistical analyses and selection of environmental variables

Statistical analyses were performed using R (R Core Team 2020). A Kruskal-Wallis rank sum test (Hollander & Wolfe 1973) was carried out in order to determine if species numbers were significantly different between trees from different sites, as well as between mountain ranges.

The ordination method, distance-based redundancy analysis (db-RDA), was used to analyze and compare epiphytic communities (Legendre & Legendre 2012; Oksanen 2012, 2015). This was performed in R with 'capscale' (package *vegan*; Legendre & Anderson 1999; Anderson & Willis 2003). Since community data were of the type presence-absence (1 or 0), the Jaccard dissimilarity index (Real & Vargas 1996) was selected to quantify the distance between communities. Constrained methods display the variation in the data of the environmental variables and are useful to test hypotheses and discover trends. In addition, permutation tests for the significance of constraints were carried out using 'anova.cca' (package *vegan*; Legendre *et al.* 2011; Legendre & Legendre 2012) with 9999 permutations. The environmental variables were standardized prior to performing the analyses. One tree from Gerakari was excluded from the final analysis because it was very different in terms of community composition to all other sampled trees since it had only four bryophyte species and no lichen species (probably due to a sampling bias) and influenced the analysis too strongly when included.

Spearman's rank correlation (Hollander & Wolfe 1973) was computed between environmental variables to check for codependent variables and exclude highly correlated (Spearman's rho > 0.7) variables that could negatively influence the reliability of the results of the distance-based redundancy analysis (Borcard *et al.* 2011). Correlation coefficients for all considered variables are found in Supplementary Material Table S1 (available online). Latitude was highly negatively correlated with longitude ($P < 0.001$, Spearman's rho = −0.93). Due to the fact that the latitudinal amplitude of the study sites was very low compared to their longitudinal amplitude (0.25° vs 1.97°), latitude was excluded from further analyses. Gridded temperature and precipitation were also excluded from further analyses due to their high correlation with longitude ($P < 0.001$, Spearman's rho = 0.88) and altitude ($P < 0.001$, Spearman's rho = 0.97), respectively, and the potential unsuitability and/or unreliability of gridded data in representing localized climatic events in the Cretan mountains due to the absence of weather stations from which to interpolate (Goedecke & Bergmeier 2018; Fazan *et al.* 2022).

Ecological indicator values

For every lichen species, the following ecological indicator values (EIVs) were obtained from Nimis (2016) and Nimis & Martellos (2021): pH of substratum, solar irradiation, aridity (i.e. air humidity), eutrophication and poleotolerance (i.e. tolerance to human disturbance). The same was achieved for mosses using the dataset of Düll (1991) for the following EIVs: light, temperature, continentality, humidity and pH of substratum.

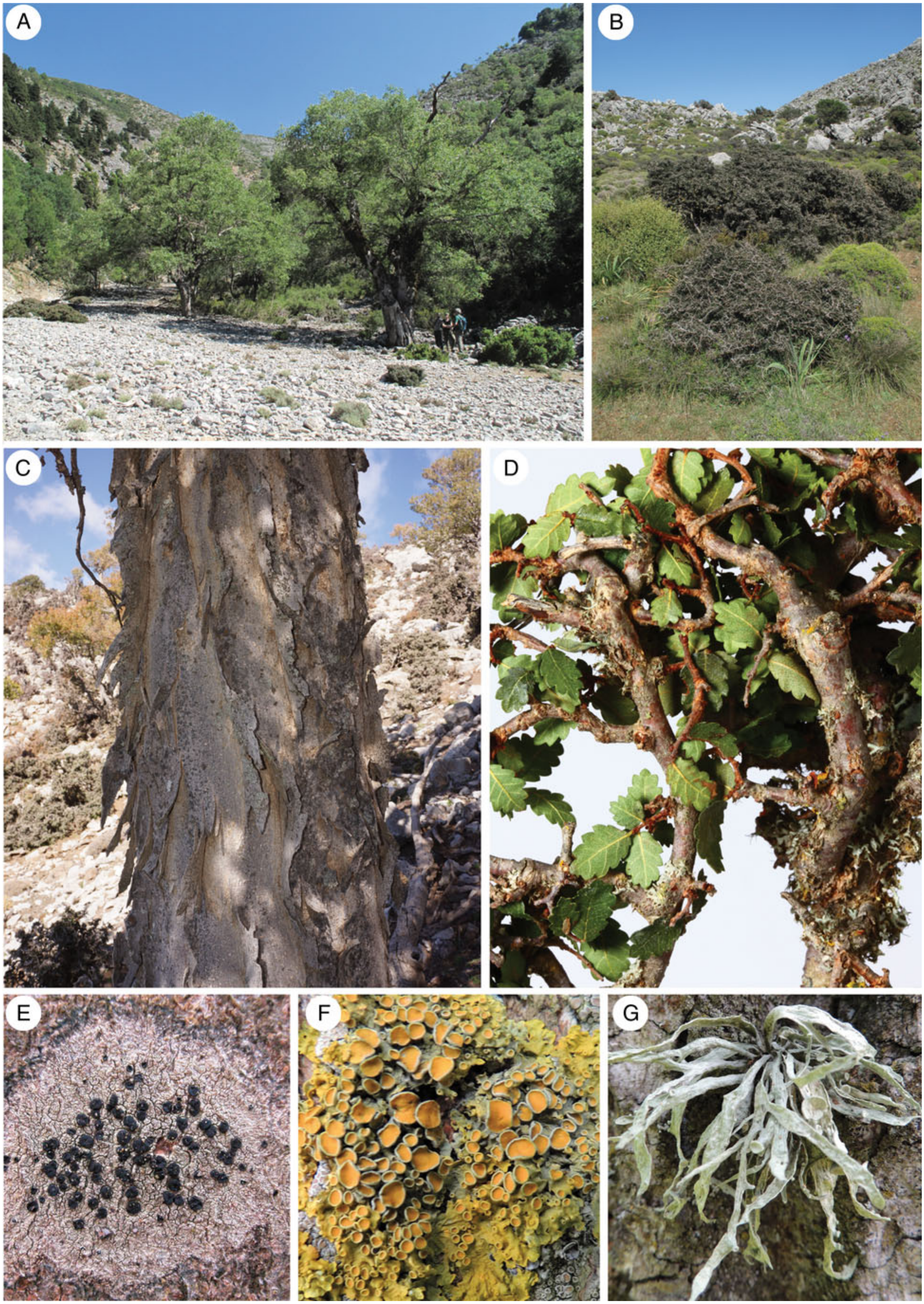

Fig. 2. A, forest fragment with large *Zelkova abelicea* trees (Omalos). B, dwarfed, heavily browsed individuals (Thripti Mts). C, trunk of a large tree with exfoliating bark (Dikti Mts). D, branches of a heavily browsed individual (Mt Kedros). Examples of different lichen growth forms: E, *Lecidella elaeochroma* (crustose). F, *Xanthoria parietina* (foliose). G, *Ramalina fraxinea* (fruticose). Photographs: G. Kozlowski (A–C), H-R. Siegel (D), W. Fałtynowicz (E–G).

Table 1. Environmental characteristics of the study sites in Crete where epiphytic material of *Zelkova abelicea* was sampled. Temp. = mean annual temperature; Prec. = average sum of annual rainfall (gridded climatic data was extracted for the period 1970–2000 from WorldClim, www.worldclim.com/version2). Browsing intensity = + moderate, ++ strong.

Mountain	Site	Latitude (DD)	Longitude (DD)	Altitude (m a.s.l.)	Topography	Browsing intensity	Temp. (°C)	Prec. (mm)
Levka Ori	Omalos	35.319010	23.918710	1160	slope	++	11.67	906
	Niato	35.287527	24.145500	1215	doline	+	12.03	954
	Impros	35.270546	24.153150	1175	slope	+	12.51	938
Kedros	Gerakari	35.194829	24.606710	1255	slope	++	12.63	1024
Psiloritis	Rouvas	35.164333	24.922790	1320	slope	++	13.07	1022
Dikti	Viannou	35.064291	25.469778	1320	slope	+	12.04	956
	Katharo	35.148004	25.567558	1160	slope	+	12.63	921
Thripti	Thripti	35.080588	25.887408	1150	doline	+	13.20	897

EIVs help to provide useful insights into the ecological niche of single species and help to evaluate the habitat quality of species assemblages (Nimis & Martellos 2001). For lichens, the values are based on ecological responses of lichens throughout their distributional range in Italy. For mosses, the EIVs focus on Central Europe and more precisely on some areas of Germany. We are aware that the ecological requirements of lichens as well as mosses occurring throughout Greece may differ. However, since no EIVs have yet been developed specifically for Greek lichens and mosses, the datasets of Düll (1991), Nimis (2016) and Nimis & Martellos (2021) appear to be the best currently available. Furthermore, Christensen (2014) argues that despite these shortcomings, the Italian dataset of ecological indicators for lichens can be applied to Greece. For lichen species that had more than one given value per indicator due to their broad ecological spectrum, the average value was computed. Values were then averaged by sampled tree and Kruskal-Wallis rank sum tests (Hollander & Wolfe 1973) were carried out for each EIV in order to see if there were significant differences between study sites.

Results

Epiphytic diversity and distribution

Overall, 70 epiphytic species were recorded on *Zelkova abelicea*: 60 lichen species belonging to 21 genera and 10 bryophyte species belonging to eight genera (Fig. 3, Tables 2 & 3). Four lichen taxa common in Greece and Europe were the most abundant: *Pleurosticta acetabulum* (found on 33 trees), *Xanthoria parietina* (30 trees), *Physcia tenella* (27 trees) and *Lecidella elaeochroma* (26 trees). All other species were recorded on 20 or fewer trees. Eighteen species occurred only once. For bryophytes, only moss species were found, and the most abundant mosses were *Leucodon sciuroides* (10 trees) and *Orthotrichum affine* (7 trees). The highest epiphytic diversity was found in Impros (42 spp.) while the lowest was found in Psiloritis (15 spp.; Fig. 4). Differences in epiphytic diversity per tree were non-significant among sites and mountains ($\chi^2 = 7.1869$, df = 7, $P = 0.4097$ and $\chi^2 = 5.898$, df = 4, $P = 0.2069$, respectively).

Ten lichen species (i.e. 17%, namely *Anisomeridium polypori*, *Candelaria concolor*, *Candelariella efflorescens*, *Huneckia pollinii*, *Ochrolechia androgyna*, *Physcia dubia*, *Physconia enteroxantha*, *Polycauliona polycarpa*, *Polyozosia populicola* and *Scoliciosporum chlorococcum* were previously unrecorded for Crete. Three of these (i.e. 5%, namely *Anisomeridium polypori*, *Candelariella efflorescens* and *Polycauliona polycarpa*) were also previously unpublished for Greece and were found in our study on two different trees in Impros and on a single tree in Thripti (Table 2). All the sampled bryophyte species have been previously recorded for Crete or Greece.

All but one of the sampled trees hosted lichens, with variable species numbers (6–20 spp., with an average of 13 lichen spp. per tree; Fig. 5A). Trees with the highest diversity of lichen species were located in the three sites of the Levka Ori, as well as in Kedros. Trees from Psiloritis, Dikti and Thripti had lower species numbers, while one tree from Gerakari (Kedros) hosted no lichens. However, differences in number of lichens per tree between sites or mountain ranges were non-significant ($\chi^2 = 4.4481$, df = 7, $P = 0.727$ and $\chi^2 = 3.6547$, df = 4, $P = 0.455$, respectively). More lichen species were recorded in the Levka Ori sites compared to the other regions (Fig. 4). With 40 species, Impros had the highest lichen diversity, followed by Omalos (33 spp.), Niato, Kedros and Viannou (27 spp.), Thripti (24 spp.), Katharo (23 spp.) and Rouvas (15 spp.) (Table 4). Overall, 53 spp. of lichen were recorded in Levka Ori compared to 35 in Dikti, 27 in Kedros, 24 in Thripti and 15 in Psiloritis (Fig. 4, Table 2). However, differences in lichen diversity between sites or mountains were not significant ($\chi^2 = 7$, df = 7, $P = 0.4289$ and $\chi^2 = 53958$, df = 4, $P = 0.249$, respectively).

Bryophytes were found only on 16 out of 36 (i.e. 44%) sampled trees, and the number of species per tree varied from 1–4 with an average of 2.25 spp. (Fig. 5B). The number of bryophytes per tree was significantly different among sites, as well as among mountain ranges ($\chi^2 = 16.166$, df = 7, $P = 0.02364$ and $\chi^2 = 13.99$, df = 4, $P = 0.007328$, respectively). Bryophytes were most abundant at Gerakari on Mt Kedros, where 8 spp. were counted, followed by Omalos and Niato (both 4 spp.), Katharo (3 spp.) and Impros (2 spp.); no bryophytes at all were recorded on trees at Rouvas, Viannou and Thripti (Fig. 4, Table 4). Total bryophyte diversity was not significantly different among sites or mountain ranges ($\chi^2 = 7$, df = 7, $P = 0.4289$ and $\chi^2 = 5.4641$, df = 4, $P = 0.2429$, respectively).

The most frequently recorded lichen thallus morphology (i.e. 52%, 31 spp.) was crustose, while 40% (24 spp.) of lichens had a foliose and only 8% (5 spp.) a fruticose thallus morphology (Table 4). Half of the 10 most abundant lichen species were

Table 2. List of the epiphytic lichens recorded on *Zelkova abelicea* in Crete showing the taxonomy, morphological type and occurrence in the study sites. The nomenclature follows Index Fungorum (Index Fungorum Partnership 2022) while the morphological type of thallus (Morph.) follows Arcadia (2022) (i.e. Cr – crustose, Fo – foliose, Fr – fruticose). Study sites (Site) are listed following a longitudinal gradient from the west to the east of Crete: O – Omalos, N – Niato, I – Impros, G – Gerakari, R – Rouvas, V – Viannou, K – Katharo, T – Thripti. Number of trees sampled per site (*n*) is also given. Species recorded for the first time in Greece are in bold, and those recorded for the first time in Crete are marked with *. (*) = species possibly recorded for the first time in Crete but treat with caution due to the uncertainty of their determination or the possible misidentification of previous Cretan records.

		Distribution							
	Site	O	N	I	G	R	V	K	T
	n	6	4	7	4	2	4	3	6
Species	Morph.								
Amandinea punctata (Hoffm.) Coppins & Scheid.	Cr	+	–	+	+	+	+	+	+
Anaptychia ciliaris (L.) Flot.	Fr	+	+	+	+	+	+	+	–
****Anisomeridium polypori*** (Ellis & Everh.) M. E. Barr	Cr	–	–	+	–	–	–	–	–
Athallia cerinella (Nyl.) Arup *et al.*	Cr	+	+	+	–	–	+	+	+
A. pyracea (Ach.) Arup *et al.*	Cr	+	+	+	+	–	+	+	+
Blastenia ferruginea (Huds.) A. Massal.	Cr	+	+	+	+	–	+	–	+
**Candelaria concolor* (Dicks.) Stein	Fo	+	+	+	–	–	–	–	–
Candelariella aurella (Hoffm.) Zahlbr.	Cr	+	–	+	+	–	–	–	–
****C. efflorescens*** R. C. Harris & W. R. Buck	Cr	–	–	+	–	–	–	–	–
C. xanthostigma (Ach.) Lettau	Cr	+	+	+	–	+	+	–	+
Collema subflaccidum Degel.	Fo	–	–	+	+	–	+	–	–
Diplotomma alboatrum (Hoffm.) Flot.	Cr	–	–	+	–	–	–	–	+
D. pharcidium (Ach.) M. Choisy	Cr	–	+	+	–	–	–	–	+
Glaucomaria carpinea (L.) S. Y. Kondr. *et al.*	Cr	+	+	+	+	–	–	–	+
**Huneckia pollinii* (A. Massal.) S. Y. Kondr. *et al.*	Cr	–	–	–	–	–	+	–	–
Lecania naegelii (Hepp) Diederich & van den Boom	Cr	+	–	+	–	–	–	+	+
Lecanora argentata (Ach.) Röhl.	Cr	+	+	–	+	–	–	–	+
L. chlarotera Nyl.	Cr	+	+	+	–	+	+	–	+
L. saligna (Schrad.) Zahlbr.	Cr	+	–	–	+	+	+	–	–
Lecidella elaeochroma (Ach.) M. Choisy.	Cr	+	+	+	+	–	+	+	+
Lepra albescens (Huds.) Hafellner	Cr	–	+	+	+	–	–	–	–
(*)*Leptogium* cf. *cochleatum* (Dicks.) P. M. Jørg. & P. James	Fo	–	–	–	–	–	+	–	–
Melanohalea exasperata (De Not.) O. Blanco *et al.*	Fo	–	+	–	–	–	–	–	–
M. laciniatula (Flagey ex H. Olivier) O. Blanco *et al.*	Fo	–	+	–	–	–	–	–	–
**Ochrolechia androgyna* (Hoffm.) Arnold	Cr	–	–	+	–	–	–	–	–
O. arborea (Kreyer) Almb.	Cr	–	–	+	–	–	–	–	–
(*)*O. szatalaensis* Verseghy	Cr	+	–	–	–	–	–	–	–
Parmelina pastillifera (Harm.) Hale	Fo	+	+	+	+	–	+	–	+
P. tiliacea (Hoffm.) Hale	Fo	–	–	–	+	+	+	+	–
Pertusaria pertusa (L.) Tuck.	Cr	–	–	–	–	+	–	+	+
Phaeophyscia nigricans (Flörke) Moberg	Fo	+	–	+	–	–	–	–	–
P. orbicularis (Neck.) Moberg	Fo	+	–	+	+	+	+	+	–
Physcia adscendens H. Olivier	Fo	+	–	–	–	–	+	–	–
P. aipolia (Ehrh. ex Humb.) Fürnr.	Fo	–	–	+	–	–	–	–	–
P. biziana (A. Massal.) Zahlbr.	Fo	–	–	+	–	–	–	–	–
**P. dubia* (Hoffm.) Lettau	Fo	–	+	+	–	–	–	–	–

(*Continued*)

Table 2. (*Continued*)

		Distribution							
	Site	O	N	I	G	R	V	K	T
	n	6	4	7	4	2	4	3	6
P. stellaris (L.) Nyl.	Fo	+	+	+	+	–	+	+	–
P. tenella (Scop.) DC.	Fo	+	+	+	+	–	+	+	+
Physconia distorta (With.) J. R. Laundon	Fo	+	–	+	+	+	+	+	–
**P. enteroxantha* (Nyl.) Poelt	Fo	–	–	–	–	–	+	–	–
P. grisea (Lam.) Poelt	Fo	+	–	+	+	+	+	–	–
P. perisidiosa (Erichsen) Moberg	Fo	–	–	+	+	+	–	+	–
P. subpulverulenta (Szatala) Poelt	Fo	–	–	+	–	+	+	+	–
P. venusta (Ach.) Poelt	Fo	+	+	+	+	–	–	+	–
Pleurosticta acetabulum (Neck.) Elix & Lumbsch	Fo	+	+	+	+	+	+	+	+
****Polycauliona polycarpa*** (Hoffm.) Frödén *et al.*	Fo	–	–	–	–	–	–	–	+
Polyozosia albescens (Hoffm.) S. Y. Kondr. *et al.*	Cr	+	–	+	+	–	+	–	–
P. dispersa (Pers.) S. Y. Kondr. *et al.*	Cr	+	–	–	–	–	–	+	–
P. hagenii (Ach.) S. Y. Kondr. *et al.*	Cr	+	–	+	–	+	–	+	+
**P. populicola* (DC.) S. Y. Kondr. *et al.*	Cr	–	–	–	+	–	–	–	–
P. semipallida (H. Magn.) Kondr. *et al.*	Cr	+	–	–	–	–	–	–	–
Pseudevernia furfuracea (L.) Zopf	Fr	+	–	–	–	–	–	–	–
Ramalina farinacea (L.) Ach.	Fr	–	+	+	+	–	–	+	+
R. fastigiata (Pers.) Ach.	Fr	–	–	+	+	–	–	–	+
R. fraxinea (L.) Ach.	Fr	+	+	–	–	–	+	+	+
Rinodina pyrina (Ach.) Arnold	Cr	+	+	+	+	–	+	+	+
R. sophodes (Ach.) A. Massal.	Cr	–	+	–	–	–	–	–	+
**Scoliciosporum chlorococcum* (Graewe ex Stenh.) Vězda	Cr	–	+	–	–	–	–	–	–
Tephromela atra (Huds.) Hafellner	Cr	–	+	–	–	–	–	+	–
Xanthoria parietina (L.) Th. Fr.	Fo	+	+	+	+	+	+	+	+

foliose, one was fruticose while the remaining four were crustose. Crustose lichens dominated in Omalos, Niato, Impros and Thripti, foliose lichens dominated in Rouvas and Viannou, and both co-occurred in Gerakari and Katharo. Fruticose lichens were always in the minority (Table 4). Half of the recorded bryophyte species were acrocarpous, the other half were pleurocarpous but with local disparities. A majority of pleurocarpous species were found in Niato and Gerakari, while acrocarpous species dominated in Katharo and no pleurocarpous species were found in Omalos. In Impros, both co-occurred (Table 4).

Influence of environmental variables on the epiphytic communities of *Zelkova abelicea*

The permutation tests for the distance-based redundancy analysis (see Supplementary Material Table S2, available online) showed that among the selected environmental variables, longitude, topography and browsing intensity were significant ($P < 0.05$) with regard to epiphytic composition, while altitude was not significant ($P = 0.21$) and was thus excluded from further analyses. Figure 6 shows the results of the distance-based redundancy analysis of epiphytic lichen and bryophyte communities on *Z. abelicea*. Several clusters of trees stand out. A first group includes all trees from Thripti. A second group includes all trees from Niato. A third group consists of five trees from Impros and one tree from Gerakari. A fourth group is composed of all individuals from Rouvas and one tree each from Viannou and Katharo. The remaining trees, and all those from Omalos, are grouped between these four clusters.

Ecological indicator values

EIVs of lichens for the eight study sites are shown in Fig. 7 and Supplementary Material Table S3 (available online). Significant, or close to significant ($P < 0.1$), differences among study sites exist for the following indicators: pH of substratum ($\chi^2 = 18.971$, df = 7, $P = 0.008$), aridity ($\chi^2 = 12.7$, df = 7, $P = 0.08$) and eutrophication ($\chi^2 = 20.743$, df = 7, $P = 0.004$).

The lichen biota living on *Z. abelicea* showed a wide range of bark pH preferences (Fig. 7A), with species tolerating very acid substrata (value 1) to species preferring basic substrata (value 5), although the most frequently distributed lichen biota showed

Table 3. List of epiphytic bryophyte species recorded on *Zelkova abelicea* with their distribution at sample sites in Crete. The nomenclature follows Ros-Espin *et al.* (2013) and the morphology follows Preston (1984) and Düll (1979). Morph. = morphological type; P – pleurocarpous, A – acrocarpous. Study sites (Site) are listed following a longitudinal gradient from the west to the east of Crete: O – Omalos, N – Niato, I – Impros, G – Gerakari, R – Rouvas, V – Viannou, K – Katharo, T – Thripti. Number of trees sampled per site (*n*) is also given.

		Distribution							
	Site	O	N	I	G	R	V	K	T
	n	6	4	7	4	2	4	3	6
Species	Morph.								
Habrodon perpusillus (De Not.) Lindb.	P	–	–	–	+	–	–	–	–
Homalothecium sericeum (Hedw.) Schimp	P	–	+	–	+	–	–	+	–
Leptodon smithii (Hedw.) F. Weber & D. Mohr.	P	–	–	–	+	–	–	–	–
Leucodon sciuroides (Hedw.) Schwägr.	P	–	+	+	+	–	–	–	–
Nogopterium gracile (Hedw.) Crosby & W. R. Buck	P	–	+	–	+	–	–	–	–
Orthotrichum affine Schrad.	A	+	–	–	+	–	–	+	–
O. lyellii Hook & Tayl.	A	+	–	–	+	–	–	+	–
O. rupestre Schleich.	A	+	+	+	–	–	–	–	–
Syntrichia laevipila Brid.	A	+	–	–	–	–	–	–	–
S. virescens (De Not.) Ochyra	A	–	–	–	+	–	–	–	–

preferences for acid to slightly basic bark conditions (values 2–4). No species linked to very shaded conditions (value 1) were found, and only one species restricted exclusively to shaded sites (value 2; *Anisomeridium polypori*) was found on one tree from Impros (Fig. 7B). All other species are light demanding species and occur in sites with diffuse light (value 3), sun exposed sites (value 4) or with very high direct solar irradiation (value 5). The majority and most frequent species are mesophytic to xerophytic species in terms of air humidity (Fig. 7C). Only two species are indicators of relatively hygrophytic conditions (value 1; *Ramalina farinacea* and *Tephromela atra*), while three species are tolerant to very arid conditions (values 4 or 5 only; *Diplotomma alboatrum*, *Diplotomma pharcidium* and *Polyozosia dispersa*). The most frequently occurring lichens were adapted to weak to high eutrophication (values 2–4; Fig. 7D). Only two species are strict indicators of no eutrophication (value 1; *Ochrolechia androgyna* and *Ochrolechia szatalaensis*), found only on three trees from Impros and one from Omalos, while six species are strict indicators of high eutrophication (values 4 or 5 only; *Candelariella efflorescens*, *Phaeophyscia nigricans*, *P. orbicularis*, *Physcia dubia*, *Physconia grisea* and *Polyozosia semipallida*). The most frequently recorded lichens have a wide poleotolerance scale (values 1–3) and tolerate anthropogenic disturbance (Fig. 7E). Species indicating low or null human disturbance were often found only on single trees. Only one species found on one tree in Viannou is indicative of old trees growing in ancient, undisturbed forest stands (value 0; *Leptogium* cf. *cochleatum*), while 10 species are strict indicators of natural or semi-natural habitats with low disturbance (value 1; *Anisomeridium polypore*, *Candelariella efflorescens*, *Huneckia pollinii*, *Melanohalea laciniatula*, *Ochrolechia androgyna*, *O. szatalaensis, Physconia venusta*, *Polyozosia populicola*, *P. semipallida* and *Ramalina fraxinea*).

EIVs for mosses for the five study sites in which mosses are present are shown in Fig. 8 and Supplementary Material Table S4 (available online). None of the differences among study sites were significant for the different EIVs. The moss species present on *Z. abelicea* are mainly light-tolerant species (value 8), although one half-shade species (value 5; *Nogopterium gracile*) and two intermediate (values 6 & 7; *Habrodon perpusillus* and *Orthotrichum lyellii*) were also present. Both Niato and Gerakari have, in addition to light-tolerant mosses, species that prefer more shaded conditions (values 5 & 6) and which were not found elsewhere. The temperature tolerance range of mosses growing on *Z. abelicea* was rather wide but most species were indicative of moderately warm conditions (values 4 & 5), with only two species indicative of rather cool conditions (values 2 & 3; *Homalothecium sericeum* and *Orthotrichum rupestre*) and two species tolerating hot to extremely hot temperatures (value 8; *Habrodon perpusillus* and *Leptodon smithii*). Gerakari was the only site in which species tolerating hot temperatures (value 8) were found, while also hosting at the same time cool and intermediate species. For continentality, all species show values between oceanic to subcontinental (values 3–5). However, species with value 3 were found only in Gerakari. Regarding humidity, species are indicative of arid conditions (values 2 & 3) to humid (values 4 & 5) but not wet conditions. The species with the highest value (5; *Habrodon perpusillus*) was found only in Gerakari, but this latter site also hosted the full range of values. As for pH of substratum, species are indicative of moderately acidic substrata (value 5) to weakly acidic to weakly basic (value 7) substrata.

Discussion

Diversity and distribution of epiphytic lichens and bryophytes

The diversity of epiphytic lichens and bryophytes growing on *Zelkova abelicea* was investigated in this study for the first time, and over the whole distribution range of the phorophyte tree species.

Our study revealed that the diversity of epiphytic lichens and bryophytes growing on *Z. abelicea* was rather high, with a total

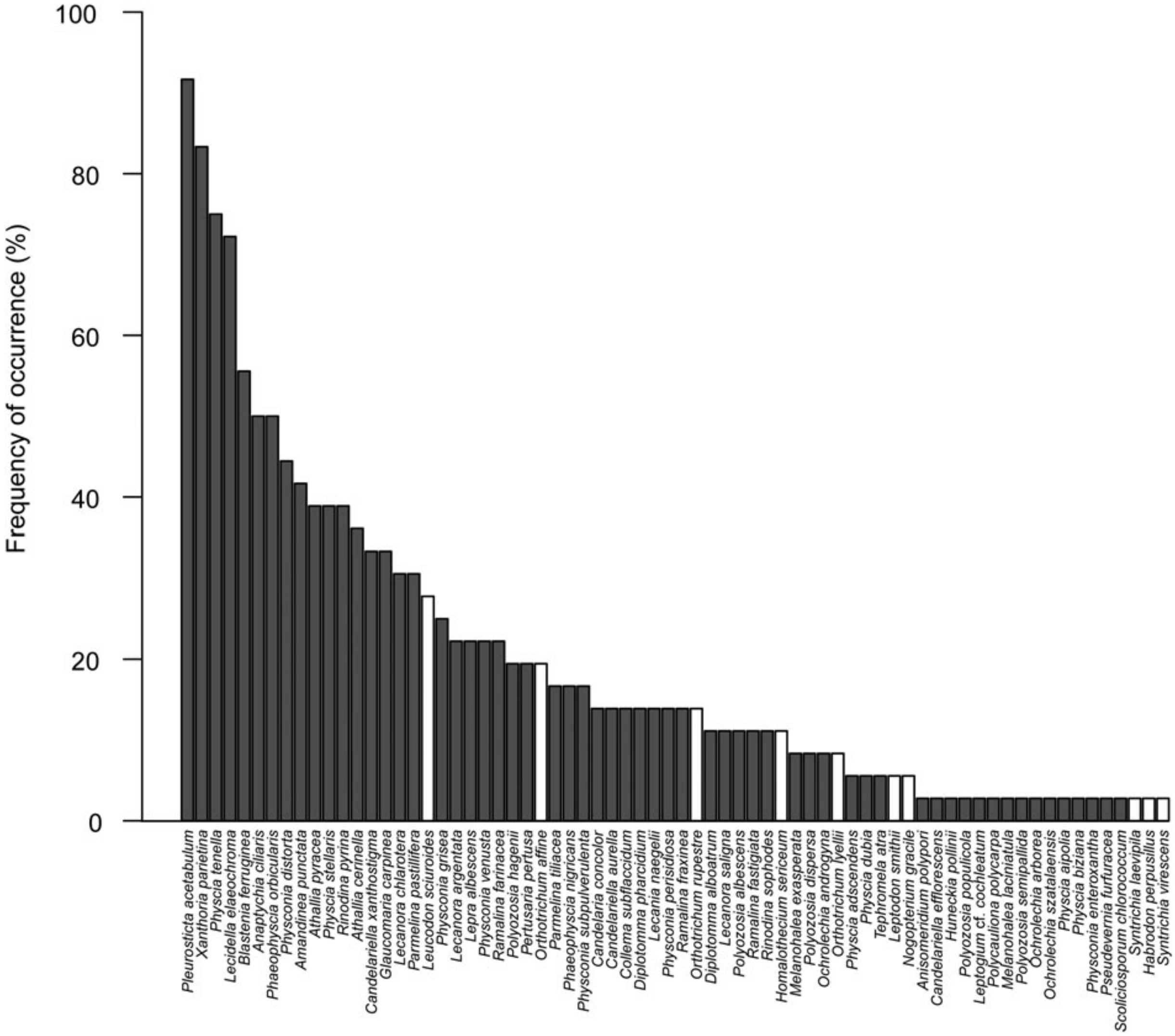

Fig. 3. Frequency of occurrence (%) of epiphytic lichens (dark grey) and bryophytes (white) growing on the investigated *Zelkova abelicea* trees on Crete.

of 70 species recorded (60 lichen and 10 bryophyte species). Individual records included up to 20 lichen and four bryophyte species per tree. All previous studies focusing on or including epiphytic lichens or bryophytes of other Cretan phorophytes reported lower species numbers (e.g. Gradstein 1971; Spribille *et al.* 2006; Christensen 2007, 2014; Vondrák *et al.* 2008). However, higher or equivalent species counts are known from several phorophytes in other areas of the Mediterranean (e.g. Zedda & Sipman 2001; Aragón *et al.* 2004). This suggests that insufficient attention has been given to Cretan epiphytes and that probably more species are still to be recorded after further in-depth sampling. Indeed, the discovery of 10 lichen species previously unrecorded for Crete, of which three are also new for the whole Greek territory, shows how little is known about the epiphytic biodiversity of phorophytes on Crete, as already emphasized by Christensen (2007, 2014). However, the present study did not reveal any epiphyte taxa exclusively restricted to *Z. abelicea* and most of the epiphytes recorded in this study are also encountered on other phorophyte species in Greece or the Mediterranean (Ros-Espin *et al.* 2013; Arcadia 2022).

The three newly reported species for Greece (*Anisomeridium polypori*, *Candelariella efflorescens* and *Polycauliona polycarpa*) are all species that are found in other nearby countries of the Mediterranean (see e.g. Yazici & Aptroot 2008; Bilovitz *et al.* 2010; Yavuz & Çobanoğlu 2018; John *et al.* 2020; Nimis & Martellos 2021), and therefore their presence in Greece is not surprising. Two other potentially new species for Crete, *Leptogium* cf. *cochleatum* and *Ochrolechia szatalaensis*, were recorded. The identity of the former is uncertain, whereas *O. szatalaensis* was considered by Kukwa (2011) to be a synonym of *O. macrospora* Vers., a species that was previously recorded from Crete by Christensen & Svane (2007). However, their specimen was reported as having large spores (68–100 µm) whereas the specimen we examined had spores that were smaller, less than 60 µm, which is typical for *O. szatalaensis*. The chemical reactions of our specimen were consistent with the diagnosis of *O. szatalaensis* reported by Kukwa (2011). Therefore, we believe that the *O. macrospora* specimen of Christensen & Svane (2007) may belong to another taxon, and that our specimen is the first record of *O. szatalaensis* for Crete, but further investigations are needed to clarify this.

Lichen and bryophyte richness is influenced by a multitude of factors which are often difficult to disentangle, such as precipitation, temperature, light, air humidity, water availability,

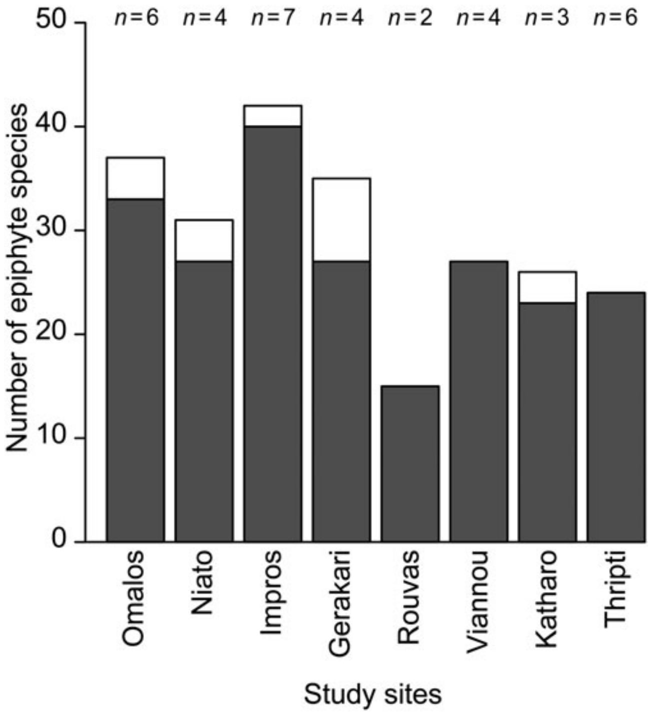

Fig. 4. Diversity of epiphytic lichen (dark grey) and bryophyte (white) species of sampled *Zelkova abelicea* trees for each of the eight study sites on Crete. n = number of trees sampled per site.

substratum characteristics, land-use and landscape history, stand structure and size, phorophyte species and surrounding vegetation (Nascimbene *et al.* 2009; Pinho *et al.* 2012; Aranda *et al.* 2014; Medina *et al.* 2014; Cardós *et al.* 2016; Henriques *et al.* 2016). Extensive pasturelands have been found to have high lichen biodiversity because of the simultaneous presence of sensitive species which would disappear in more eutrophicated sites, and of nitrophytic species associated with locally higher atmospheric ammonia due to the activity of grazing animals (Śliwa 2006; Pinho *et al.* 2012). Tree age is known to be an important factor in sustaining lichen and bryophyte biodiversity since epiphytes have had more time to establish on older trees and/or because of age-dependent changes in bark qualities (Johansson *et al.* 2007; Ranius *et al.* 2008; Fritz *et al.* 2009; Lie *et al.* 2009; Nascimbene *et al.* 2009; Király *et al.* 2013). A study of the demographic structure of *Z. abelicea* populations showed that not only arborescent trees but also dwarfed individuals can be several centuries old (Fazan *et al.* 2012), and thus dwarfed individuals may act as important, but often overlooked, phorophytes.

There were also spatial patterns of richness. *Zelkova abelicea* of the Levka Ori mountain range show the highest diversity of epiphytes since 53 out of 60 species of lichen and 7 out of 10 species of bryophyte were found there. However, this may be expected since the highest number of trees (17 trees, i.e. 47% of the total), including both arborescent and dwarfed individuals, was sampled there. This mountain range (with its suitable climatic conditions; Goedecke & Bergmeier 2018) hosts the most developed and abundant number of *Z. abelicea* stands (Kozlowski *et al.* 2014) and Cardós *et al.* (2016) has found that well-developed and large tree stands tend to have higher lichen and bryophyte diversity than small, fragmented or isolated tree patches. Furthermore, in the Levka Ori, a higher lichen diversity than elsewhere was found on individual trees, with up to 20

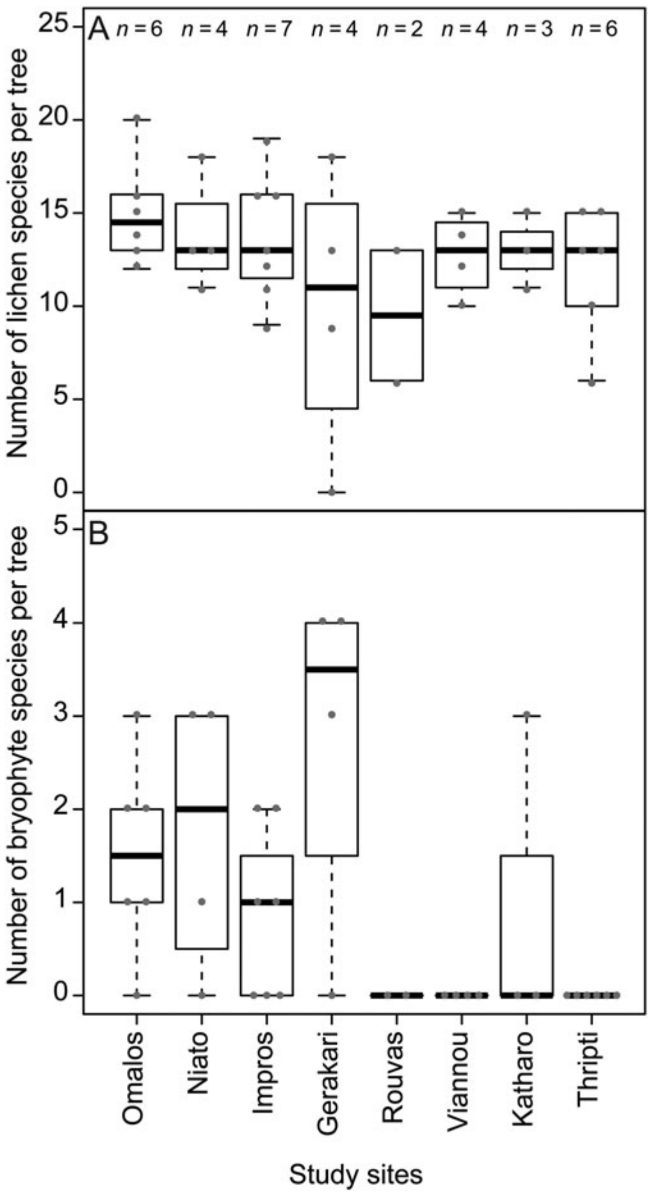

Fig. 5. Boxplots of the number of lichen (A) and bryophyte (B) species found on *Zelkova abelicea* trees in each of the eight study sites on Crete. n = number of trees per site. Grey dots represent individual trees. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range.

species per tree (Fig. 5). There are no previous comparisons of epiphytic flora between mountain ranges of Crete. However, Christensen (2014) found a higher diversity of lichens on *Platanus orientalis* L. in western Crete compared to trees situated in central Crete, which he attributed to the higher precipitation occurring in western Crete compared to more eastern sites, and in some cases also differences in land-use practices. The Levka Ori is the highest rainfall area of the island (Varouchakis *et al.* 2018; Agou *et al.* 2019) and an increased lichen diversity due to a positive correlation with precipitation has also been noticed by other researchers (e.g. Giordani 2006; Svoboda *et al.* 2010).

With regard to the bryophyte flora, Gerakari on Mt Kedros appears to be the most suitable place in our study and contained by far the highest diversity of bryophytes, with eight out of 10 species recorded there, as well as the highest number of bryophytes

Table 4. Proportion in percentage of lichens and bryophytes recorded on Cretan *Zelkova abelicea* trees per site. The number of epiphytes per site is given in brackets. Thallus morph. = proportion of lichens based on the morphological form of their thallus (Cr – crustose, Fo – foliose, Fr – fruticose). Morph. = proportion of bryophytes based on their morphology (P – pleurocarpous, A – acrocarpous).

		Overall (%)		Lichens (%)			Bryophytes (%)	
		Epiphytes		Thallus morph.			Morph.	
Mountain	Site	Lichens	Bryophytes	Cr	Fo	Fr	P	A
Levka Ori	Omalos	89 (33)	11 (4)	55	36	9	0	100
	Niato	87 (27)	13 (4)	52	37	11	75	25
	Impros	95 (40)	5 (2)	50	42.5	7.5	50	50
Kedros	Gerakari	77 (27)	23 (8)	44.5	44.5	11	62.5	37.5
Psiloritis	Rouvas	100 (15)	0	40	53	7	-	-
Dikti	Viannou	100 (27)	0	41	52	7	-	-
	Katharo	88 (23)	12 (3)	43.5	43.5	13	33	67
Thripti	Thripti	100 (24)	0	66.5	21	12.5	-	-

per tree. On Mt Kedros, the sampling site is located in an open forest on a steep and shaded north-facing slope at the foot of a cliff. This site has a relatively high precipitation and high potential run-off or percolation (Goedecke & Bergmeier 2018) and had the lowest heat load value (following McCune & Keon 2002) of all analyzed *Z. abelicea* sites, conditions that seem to be favourable to the development of a rich moss community.

The lowest epiphytic diversity (only 15 species of lichen and no bryophytes) was found at Rouvas on Mt Psiloritis, although this is also the site in which the lowest number of trees ($n = 2$) was sampled. Some areas of Mt Psiloritis have been previously found to have a low number of endemic vascular species due to a supposedly stronger human impact on the vegetation there than elsewhere (Legakis & Kypriotakis 1994). This strong anthropogenic impact coupled with locally adverse microclimatic conditions could account for the low epiphytic diversity recorded for this area.

Only mosses and no liverworts were found during our study. This almost certainly reflects the more pronounced drought intolerance of most epiphytic liverworts (Bischler 2004). Three of the four most frequently recorded bryophyte species have a widespread distribution in temperate Europe (Düll 1984, 1985). The largest areas on the trunks of *Z. abelicea* were occupied by *Leucodon sciuroides* which was also the most frequently recorded species. Several of the less frequently recorded bryophytes are oceanic or sub-oceanic species (Düll 1984, 1985) and occur throughout the Mediterranean basin (Ros-Espin *et al.* 2013). The majority of bryophytes growing on the trunk of *Z. abelicea* trees are light-loving species (Düll 1991) and are not found in densely forested areas.

Bryophytes did not occur at all in three sites (Rouvas, Viannou, Thripti), all situated in central or eastern Crete, whereas all sites in western Crete recorded bryophytes. With the exception of Katharo, all sampled trees east of Mt Kedros hosted no bryophytes. As suggested for the lichen flora, Gradstein (1971) evokes the west-east decreasing gradient in precipitation as a major factor influencing the distribution of bryophytes in Crete, although in his study some bryophytes were found uniquely in the central or eastern Cretan mountains. This explanation seems to be verified by our study. It is possible that the three sites without epiphytic bryophytes present environmental conditions that are not suitable for their growth, although further field investigations and more in-depth sampling should be undertaken to confirm this finding. Katharo stands out amongst the other eastern sites because the sampled trees were located on the border of a cultivated plateau, and thus epiphytic bryophytes there could possibly benefit from agricultural activities or moisture due to irrigation.

Factors influencing the species composition of epiphytic communities on Zelkova abelicea

The permutation tests for the db-RDA showed that longitude, topography and browsing pressure were significant in differentiating epiphytic communities whereas altitude was not. The db-RDA showed that the three sites of Impros, Niato and Thripti were clearly distinguished in terms of composition of epiphytic community. Moreover, Rouvas with the addition of one tree from Viannou and one from Katharo were also differentiated.

Altitude was not significant in influencing species composition of the epiphytic community, despite the fact that it is known, alongside precipitation, to be a major factor influencing species composition in the Mediterranean (see e.g. Loppi *et al.* 1997; Mucina *et al.* 2000; Matos *et al.* 2014; Medina *et al.* 2014; Vieira *et al.* 2016; Sevgi *et al.* 2019). This is probably because all investigated sites were situated within a narrow altitudinal range (i.e. only 170 m between the highest and lowest sites). Furthermore, longitude, or geographical position on Crete, is highly reflective of precipitation patterns, with a general west to east decreasing trend (Varouchakis *et al.* 2018; Agou *et al.* 2019), although small-scale climatic conditions such as orographic effects, cloud and dew accumulation and snow cover (see Goedecke & Bergmeier 2018) also probably play an important role. Niato and Impros have completely different precipitation patterns despite being geographically close (Fig. 1). Niato is located on the windward side of the Levka Ori, in a doline surrounded by mountains where pockets of fog may persist and in an area which receives abundant levels of rainfall. Impros is on the dry leeward southern side of the same mountain range, on a slope overlooking the Libyan Sea. The importance of nocturnal dew or humidity rising from the sea is unknown for all sites and might be an important and overlooked factor that explains the compositional differences between these nearby sites. Indeed, the lichen community of Impros, although showing a wide

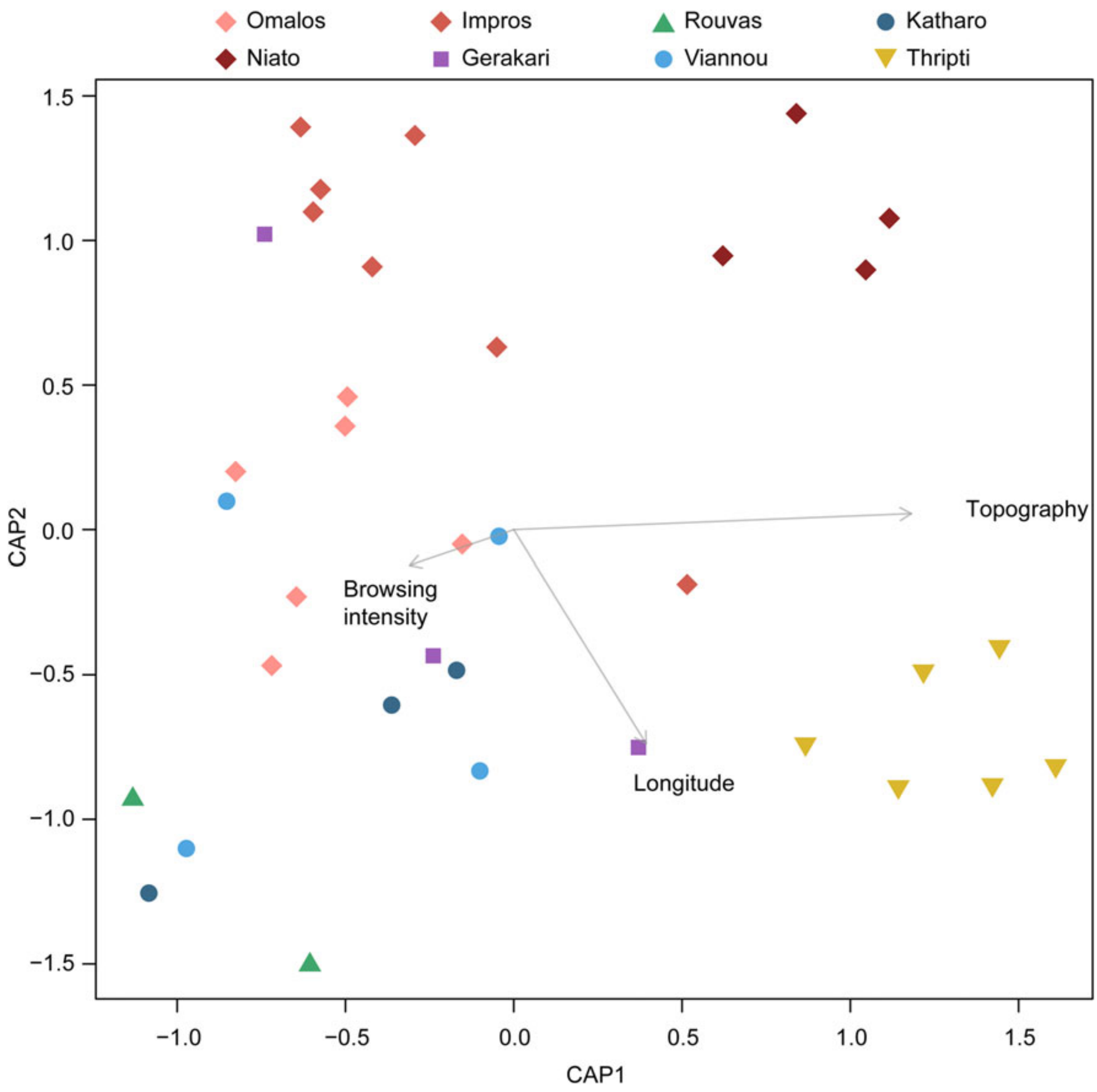

Fig. 6. Ordination plot of the distance-based redundancy analysis of epiphytic lichen and bryophyte communities on *Zelkova abelicea* trees on Crete. Each symbol represents the community found on a single *Z. abelicea* tree. Each mountain range is represented by a different shape (◆ Levka Ori, ■ Mt Kedros, ▲ Mt Psiloritis, ● Dikti Mts, ▼ Thripti Mts) and each study site by a different colour. Significant environmental variables are fitted (represented by arrows). Arrow lengths are proportional to the significance of the variables in the permutation test.

range of EIVs, includes several lichen taxa that are highly sensitive to air humidity and solar irradiation (Fig. 7 and see below).

Local effects such as topography (i.e. slope or doline) may also play an important role in community composition. Niato and Thripti are the only two sampling sites situated on a flat mountain doline and not on a slope. However, coincidentally, these two sites were the only two places visited during the study where no arborescent trees were found, and thus only dwarfed shrubby *Z. abelicea* individuals were sampled. As a result, we cannot disentangle the influence of topography from that of tree morphology here. However, dolines have different pedological conditions (e.g. deeper soils, different soil pH and nutrient content) than sloped areas (Egli 1993) and dwarfed individuals have a different architecture than arborescent trees; the former may host epiphytic lichens and bryophytes found necessarily closer to the ground and living under different microclimatic and biotic (e.g. browsing) influences. Dwarfed trees or otherwise low-growing shrubs seem to have been often overlooked in previous studies. Here, neither Niato nor Thripti showed lower epiphytic species numbers compared to other sites where arborescent trees were sampled. This is particularly true for Niato where 31 lichen species and four bryophyte species were found, showing a relatively high overall diversity. These results underline the importance of dwarfed, overbrowsed individuals as refugia for epiphytic floras. This is consistent with the results of Spribille *et al.* (2006) who found species-rich epiphytic lichen communities on trees in overbrowsed and dwarfed communities, and of Grube *et al.* (2001) who state that thorny cushion plants provide interesting microhabitats for epiphytic lichens. Moreover, Pirintsos *et al.* (1998) showed that lichen community composition in overbrowsed dwarfed shrublands was influenced mainly by shrub height and shrub density (i.e. gaps between shrubs) which influence microclimatic conditions for lichen growth, but also depended on the phorophyte species present. Furthermore, epiphytic lichen communities have been found to change depending on the height at which they grew on the trunk (e.g. Pirintsos *et al.* 1993;

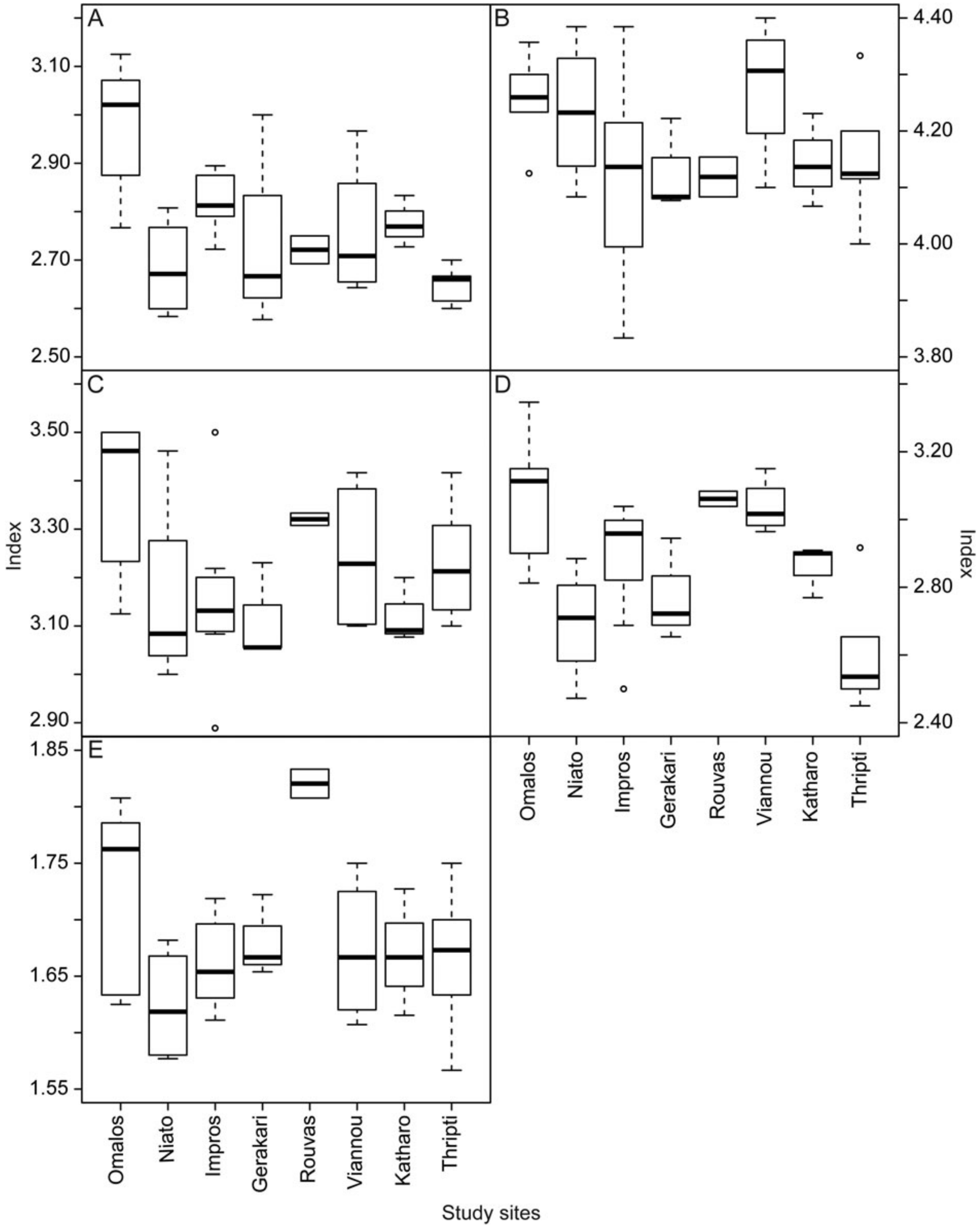

Fig. 7. Ecological indicator values for lichens recorded on *Zelkova abelicea* trees at different study sites on Crete following Nimis (2016) and Nimis & Martellos (2021). Detailed information is found in these publications and Supplementary Material Table S3 (available online). Only the observed values are described here. A, pH of substratum; 2 = acid substrata, 3 = subacid to subneutral substrata, 4 = slightly basic substrata. B, solar irradiation; 3 = in sites with plenty of diffuse light but scarce direct solar irradiation, 4 = in sun-exposed sites without extreme solar irradiation, 5 = in sites with very high direct solar irradiation. C, aridity (air humidity); 2 = rather hygrophytic, intermediate between 1 and 3, 3 = mesophytic, 4 = xerophytic but absent from extremely arid stands. D, eutrophication (including deposition of dust and nitrogen compounds); 2 = resistant to very weak eutrophication, 3 = resistant to weak eutrophication, 4 = occurring in rather highly eutrophicated situations. E, poleotolerance (i.e. tolerance to human disturbance); 1 = species occurring in natural or semi-natural habitats, 2 = species occurring in moderately disturbed areas (e.g. agricultural areas, small settlements, etc.). The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range while values exceeding this threshold are plotted as open circles.

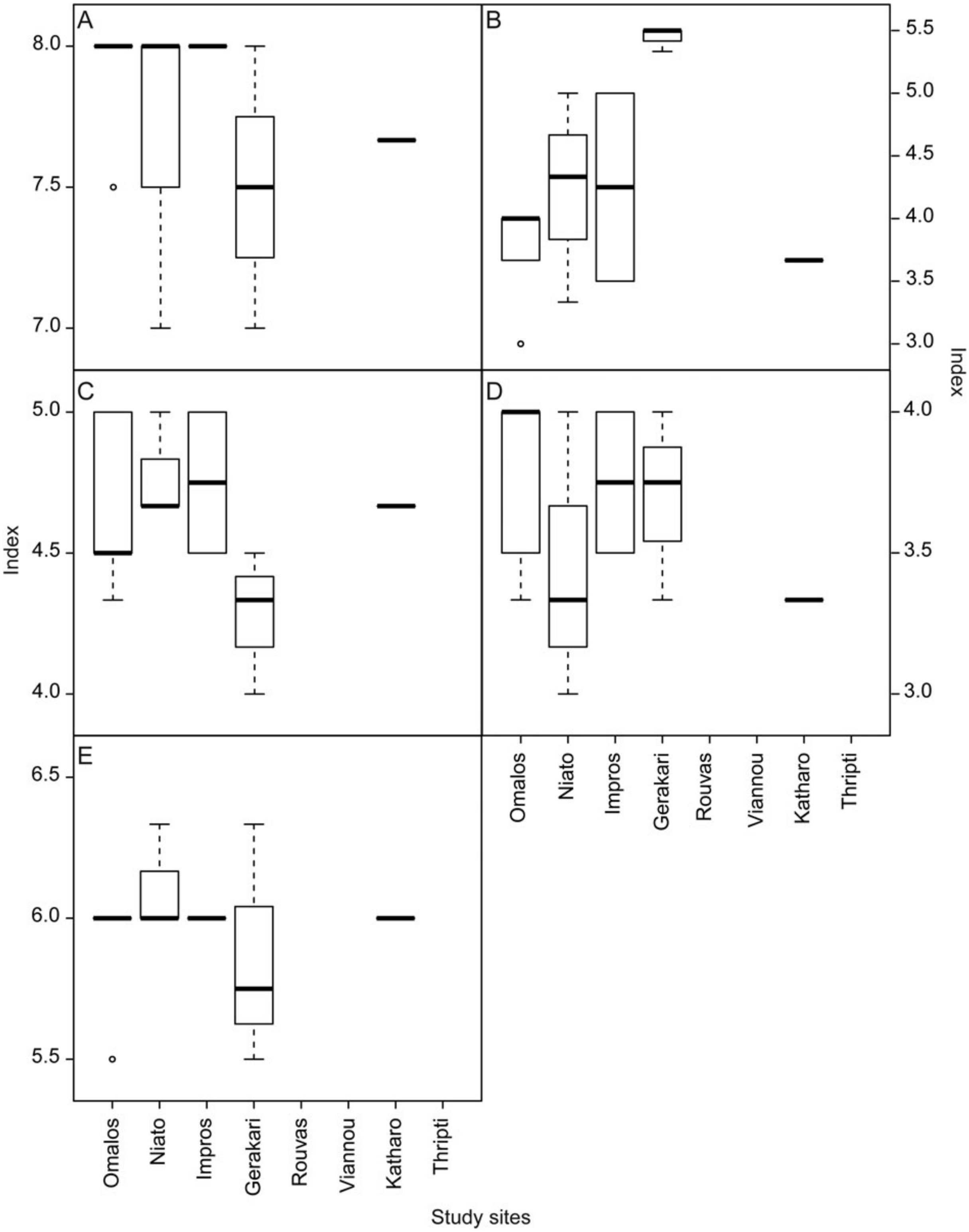

Fig. 8. Ecological indicator values for mosses recorded on *Zelkova abelicea* trees at different study sites on Crete following Düll (1991). Detailed information can be found in that publication and Supplementary Material Table S4 (available online). Only the observed values are described here. A, light; 5 = half-shade, 6 = between 5 and 7, 7 = half-light, 8 = light. B, temperature; 1 = cold, 2 = between 1 and 3, 3 = cool, 4 = between 3 and 5, 5 = moderately warm, 6 = between 5 and 7, 7 = warm. C, continentality; 2 = oceanic, 3 = between 2 and 4, 4 = suboceanic, 5 = intermediate. D, humidity; 1 = strongly arid, 2 = between 1 and 3, 3 = arid, 4 = between 3 and 5, 5 = humid. E, pH of substratum; 5 = moderately acidic, 6 = between 5 and 7, 7 = weakly acidic to weakly basic. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range while values exceeding this threshold are plotted as open circles.

Asplund *et al.* 2014). Epiphytic communities living on dwarfed *Z. abelicea* individuals may benefit from microclimatic conditions linked with this specific tree morphology and which are probably different to those of arborescent trees. Despite their small size, dwarfed *Z. abelicea* individuals were also found to be in some cases older than arborescent trees (Fazan *et al.* 2012), and old trees are known to have more developed and more species-rich epiphyte communities (Nascimbene *et al.* 2010). This could be explained by the fact that they offer more diverse microhabitats (Nordén *et al.* 2018), provide more time for the colonization and establishment of species-rich communities or possess different substratum qualities (Lie *et al.* 2009). Nevertheless, our study contains a bias, since epiphytes were collected only from the trunk on arborescent trees and not from the canopy, while being collected from both the trunk and canopy of dwarfed individuals. Trunk and canopy epiphytic communities have been shown to be quite different in many cases (e.g. McCune *et al.* 2000; Ellis 2012; Maceda-Veiga & Gómez-Bolea 2017), and therefore further sampling should be undertaken to assess if this could also be the case for *Z. abelicea* and whether this could lead to different results than those presented here.

Ecological indicator values

Since no database including Greece has been compiled so far, the EIVs used in this study were those compiled for Italy (lichens) and Central Europe (mosses). Some authors have successfully used EIVs for vascular plants outside of their original range (e.g. Körner *et al.* 1997). In addition, Christensen (2014) argues that, at least for lichens, the Italian database can also be used in a Greek context. However, other authors (e.g. Godefroid & Dana 2006) have shown differences in EIVs for vascular plants between Mediterranean countries, and this is important to keep in mind when interpreting the data presented in this paper.

Significant differences in lichen assemblages in terms of bark pH, air humidity and eutrophication were recorded among sites. These differences are most probably related to variations in intensity of pastoral activities. Indeed, an increased presence of browsing animals will trigger a rise in eutrophication levels through higher deposition of nitrogen which in turn will raise bark pH. Bark pH is known to be an important factor in determining epiphytic lichen composition (van Herk 2001) and will increase through the emission of ammonia (NH_3) as a result of practices such as animal husbandry (Paoli *et al.* 2010), but also due to dust deposition and dry conditions (Loppi & De Dominicis 1996; Loppi *et al.* 1997). However, bark pH also depends on phorophyte species, tree age, position of epiphytes on the tree and soil type (Kermit & Gauslaa 2001). Paoli *et al.* (2010) state that due to the intense and widespread livestock grazing that occurs throughout Crete, the whole island is affected to some extent by habitat eutrophication through the deposition of nitrogen, but it is clear that local disparities exist among sites. Furthermore, the presence of species tolerant to lower air humidity in some areas may be explained not only by more xeric growth conditions but also by the prevalence of nitrogen-tolerant species, since nitrogen-sensitive species are also often sensitive to air humidity (Hauck & Wirth 2010).

Despite the effects of grazing and localized eutrophication, Pinho *et al.* (2012) found that extensive pasturelands could maintain high lichen species diversity due to the concomitant presence of nitrophilous and non-nitrophilous (sensitive) lichen species. However, the maintenance of the latter, albeit with a decrease in abundance, occurs only up to a certain degree of land use intensity, after which these species disappear. This phenomenon can be observed, for example, in Omalos where lichen assemblages signal the highest values of bark pH and aridity, rather high values of eutrophication and high values of poleotolerance. This all tends to point toward a strong influence of pastoral activities on the local lichen assemblages, with the predominance of eutrophication- and poleotolerant species. The values of aridity that are higher than elsewhere and the high proportion of nitrogen-tolerant species are probably linked in Omalos. However, the presence of species such as *Ochrolechia szatalaensis*, a strict indicator of no eutrophication, and of several species with low poleotolerance or low to medium aridity tolerance demonstrates that sensitive species can still be maintained locally, and possibly thrive in Cretan *Z. abelicea* stands.

No significant differences were found between sites when considering the EIVs of mosses, but most sites contained only a small number of species, from which it is difficult to extract conclusions. Nevertheless, compared to the other study sites, Gerakari showed a moss community that included, besides generalists, more shade-tolerant species, oceanic species and species tolerating less arid conditions. Although these features could be a sampling artefact since Gerakari also hosts the highest number of moss species (8 out of 10 species), it is probably reflective of local site conditions. Indeed, Gerakari also hosts lichen species indicative of higher air humidity in comparison with the rest of the study sites. These findings are probably due to the fact that the site is situated on a shaded north-facing slope at the foot of a cliff. Goedecke & Bergmeier (2018) previously stated that the site had the lowest heat load value of all analyzed *Z. abelicea* sites.

The sites of Niato, Thripti and to a lesser extent Impros have some particularities in terms of lichen EIVs and confirm the db-RDA results (Fig. 6). Niato and Thripti show lower values of bark pH and eutrophication. In addition, Niato has a lichen assemblage that is more sensitive to air humidity and human disturbance than Thripti, although the latter also contains lichens that are very sensitive to human disturbance. At Impros, lichen EIVs point towards a wider range of tolerance to solar irradiation compared to all other sites. Both lichens preferring more shaded conditions and lichens tolerant to high solar irradiation are found there. These findings could reflect the dwarfed nature of some of the sampled trees (Niato and Thripti) but could also be an indicator of lower than expected pastoral activities, possibly resulting from the remoteness of the three sites.

Rouvas, on the contrary, seems to have lost its most sensitive lichens. The site is distinguished by the low number of lichen species (only 15 spp.) found there, an absence of bryophytes as well as its levels of poleotolerance that are higher than elsewhere, comparatively high eutrophication level and presence of lichens tolerating high air aridity levels. These results might be explained by a locally sparser forest cover, a more arid environment or, as suggested by Legakis & Kypriotakis (1994), Lyrintzis (1996) and Hostert *et al.* (2003), could be indicative of a stronger disturbance than elsewhere due to locally intensive agropastoral practices or other human activities. In our study, the site of Rouvas seems to be the least favourable site for epiphytic lichens on *Z. abelicea*, although sampling more trees in Rouvas would be needed to confirm this finding.

Conclusions

The diversity and distribution of epiphytic lichens and bryophytes using *Zelkova abelicea* as a phorophyte were studied for the first time over the whole distribution range of this tree species. The rather high diversity of epiphytes recorded and the number of previously unrecorded species for Greece and Crete alike show how much is still unknown about epiphytes on Crete in general, but also about the epiphytic communities hosted by *Z. abelicea*. Differences in community composition and species diversity between sites was reflective of many differences in local conditions, across scales relating to climate, topography, land use, pastoral activities and tree morphology (dwarfed or arborescent). Our study also highlighted the importance of possibly very old, dwarfed trees as key hosts of specific epiphytic communities. Dwarfed trees were found to have different but equally rich communities as arborescent *Z. abelicea* trees. We were able to show that although some areas seem to experience a relatively strong influence of human activities, they nevertheless maintained a high diversity of species due to the co-occurring presence of both eutrophication-tolerant and -sensitive species. Our study paves the way for further and more in-depth research to explain the patterns observed.

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Author ORCIDs. Laurence Fazan, 0000-0002-2981-1806; Yann Fragnière, 0000-0003-4167-379X; Dariusz J. Gwiazdowicz, 0000-0002-0064-2316; Wiesław Fałtynowicz, 0000-0003-3636-6218; Dany Ghosn, 0000-0003-1898-9681; Paweł Urbański, 0000-0002-5199-8021; Guiseppe Garfì, 0000-0003-0466-4288; Salvatore Pasta, 0000-0003-3265-9072; Gregor Kozlowski, 0000-0003-4856-2005.

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Supplementary material

Table S1. Spearman's rank correlation rho values for selected environmental variables. Significance levels: ***p<0.001, **p<0.01, *p<0.1.

	Longitude	Altitude	Topography	Browsing intensity	Temperature	Precipitation
Latitude	-0.93***	-0.09	-0.16	0.47**	-0.70***	-0.08
Longitude	-	-0.18	0.31*	-0.47**	0.88***	-0.14
Altitude	-	-	-0.39*	0.11	-0.27	0.97***
Topography	-	-	-	-0.43*	0.31*	-0.39*
Browsing intensity	-	-	-	-	-0.31*	0.15
Temperature	-	-	-	-	-	-0.16
Precipitation	-	-		-	-	-

Table S2. Permutation tests of the distance-based redundancy analysis. Significant p<0.05 values are given in bold.

Environmental variable	Df	Sum of squares	F statistic	Probability (>F)
Longitude	1	0.6196	2.4941	**0.0001**
Topography	1	0.9195	3.7015	**0.0001**
Browsing intensity	1	0.4004	1.6117	**0.0320**
Altitude	1	0.3020	1.2158	0.2143
Residual	30	7.4527		

Table S3. Ecological indicator values taken from Nimis (2016) and Nimis & Martellos (2021) for the observed lichens. pH: pH of substratum. 1: very acid substrata, 2: acid substrata, 3: subacid to subneutral substrata, 4: slightly basic substrata, 5: basic substrata. Solar irradiation. 1: in very shaded situations, 2: in shaded situations, 3: in sites with plenty of diffuse light but scarce direct solar irradiation, 4: in sun-exposed sites but avoiding extreme solar irradiation, 5: in sites with very high direct solar irradiation. Aridity (air humidity). 1: hygrophytic, in sites with a very high frequency of fog, 2: rather hygrophytic, intermediate between 1 and 3, 3: mesophytic, 4: xerophytic but absent from extremely arid stands, 5: very xerophytic. Eutrophication (including deposition of dust and nitrogen compounds). 1: not resistant to eutrophication, 2: resistant to very weak eutrophication, 3: resistant to weak eutrophication, 4: occurring in rather high eutrophicated situations, 5: occurring in very highly eutrophicated situations. Poleotolerance, i.e. tendency of a lichen to occur in areas with different degrees of human disturbance. 0: species occurring exclusively on old trees in ancient, undisturbed forests, 1: species occurring in natural or semi-natural habitats, 2: species occurring in moderately disturbed areas, 3: species occurring in heavily disturbed areas. Altitudinal distribution. 1: eu-Mediterranean belt, 2: submediterranean belt, 3: montane belt, 4: Oroboreal belt of the Alps, 5: above treeline.

Species	pH	Solar irradiation	Aridity	Eutrophication	Poleotolerance	Altitude
Amandinea punctata	123	45	34	234	123	1234
Anaptychia ciliaris	23	45	3	23	12	123
Anisomeridium polypori	34	2	2	12	1	123
Athalia cerinella	23	45	34	34	12	123
Athalia pyracea	34	45	34	234	12	1234
Blastenia ferruginea	23	45	3	123	12	123
Candelaria concolor	34	45	34	345	123	123
Candelariella aurella	45	345	345	234	123	12345
Candelariella efflorescens	34	45	3	45	1	123
Candelariella xanthostigma	23	345	3	23	123	1234
Collema subflaccidum	23	34	2	23	12	123
Diplotomma alboatrum	34	45	45	34	12	123
Diplotomma pharcidium	34	45	45	34	12	12
Glaucomaria carpinea	23	345	34	123	123	1234
Huneckia pollinii	23	45	34	23	1	12
Lecania naegelii	23	4	3	123	12	123
Lecanora argentata	23	34	3	12	12	234
Lecanora chlarotera	23	345	34	2345	123	1234
Lecanora saligna	12	45	4	12	12	234
Lecidella elaeochroma	234	345	2345	234	123	1234
Lepra albescens	23	34	23	123	12	1234
Leptogium cf. *cochleatum*	23	3	2	12	0	123
Melanohalea exasperata	23	45	34	23	12	123
Melanohalea laciniatula	12	3	2	23	1	23
Ochrolechia androgyna	12	3	2	1	1	2345
Ochrolechia arborea	2	34	3	123	12	23
Ochrolechia szatalaensis	12	3	23	1	1	34
Parmelina pastillifera	23	4	2	23	12	234
Parmelina tiliacea	2	34	3	23	123	1234
Pertusaria pertusa	2	3	23	12	12	1234
Phaeophyscia nigricans	34	45	34	4	12	23
Phaeophyscia orbicularis	2345	345	34	45	123	1234
Physcia adscendens	2345	45	34	345	123	12345
Physcia aipolia	23	45	3	34	123	1234
Physcia biziana	23	45	34	34	123	12
Physcia dubia	234	45	4	45	123	12345
Physcia stellaris	23	45	3	234	12	234
Physcia tenella	234	45	34	34	12	123
Physconia distorta	34	45	34	34	123	123
Physconia enteroxantha	23	45	3	34	12	123
Physconia grisea	34	345	3	45	123	1234
Physconia perisidiosa	23	34	23	23	12	123
Physconia subpulverulenta	3	45	3	34	12	12
Physconia venusta	23	34	2	12	1	23
Pleurosticta acetabulum	23	45	34	23	12	1234
Polycauliona polycarpa	23	45	34	23	12	34
Polyozosia albescens	345	345	345	34	123	1234
Polyozosia dispersa	45	345	45	234	23	123
Polyozosia hagenii	345	45	345	234	123	1234
Polyozosia populicola	23	34	3	1234	1	3
Polyozosia semipallida	45	45	34	45	1	2345
Pseudevernia furfuracea	12	345	34	12	12	234
Ramalina farinacea	23	345	12	12	12	1234
Ramalina fastigiata	23	345	23	123	12	1234
Ramalina fraxinea	23	45	23	23	1	23
Rinodina pyrina	23	45	3	23	12	123
Rinodina sophodes	23	45	34	12	12	1234
Scoliciosporum chlorococcum	123	23	23	123	12	1234
Tephromela atra	23	34	123	12	123	12345
Xanthoria parietina	234	345	34	34	123	1234

Table S4. Ecological indicator values for the observed bryopyhtes. The ecological indicator values follow Düll (1991). Li: light, 1: deep shade, 2: between 1 and 3,. 3: shade, 4: between 3 and 5, 5: half-shade, 6: between 5 and 7, 7: half-light, 8: light, 9: full light, Te: temperature, 1: cold, 2: between 1 and 3, 3: cool, 4: between 3 and 5, 5: moderately warm, 6: between 5 and 7, 7: warm, 8: between 7 and 9, 9: extremely warm, Co: continentality, 1: euoceanic, 2: oceanic, 3: between 2 and 4, 4: suboceanic, 5: intermediate, 6: subcontinental, 7: between 6 and 8, 8: continental, 9: eucontinental, Hu: humidity, 1: strongly arid, 2: between 1 and 3, 3: arid, 4: between 3 and 5, 5: humid, 6: between 5 and 7, 7: wet, 8: between 7 and 9, 9: on lasting wet places near water or streams as well as regularly flooded or submerged mosses, Re: Reaction (pH): 1: strongly acidic, 2: between 1 and 3, 3: acid, 4: between 3 and 5, moderately acid, 6: between 5 and 7, 7: weakly acid, 8: between 7 and 9, 9: basic and calcareous.

Species	Ecological indicator values				
	Li	Te	Co	Hu	Re
Habrodon perpusillus	6	8	3	5	5
Homalothecium sericeum	8	3	5	2	7
Leptodon smithii	8	8	3	4	6
Leucodon sciuroides	8	5	5	4	6
Nogopterium gracile	5	5	4	4	5
Orthotrichum affine	8	4	5	4	6
Orthotrichum lyellii	7	4	4	4	5
Orthotrichum rupestre	8	2	4	3	6
Syntrichia laevipila	8	5	4	3	6
Syntrichia virescens	8	5	5	2	6

Table S5. Raw presence-absence occurrences of lichen and bryophyte species found growing on *Z. abelicea* trees on Crete. Mountain: L: Levka Ori, K: Kedros, P: Psiloritis, D: Dikti, T: Thripti. Site: Oma: Omalos, Nia: Niato, Imp: Impros, Ger: Gerakari, Rou: Rouvas, Via: Viannos, Kat: Katharo, Thr: Thripti. Epiphyte type: L: lichen, M: moss (*to be continued…*).

Sample / tree ID	Mountain	Site	*Amandinea punctata*	*Anaptychia ciliaris*	*Anisomeridium polypori*	*Athallia cerinella*	*Athallia pyracea*	*Blastenia ferruginea*	*Candelaria concolor*	*Candelariella aurella*	*Candelariella efflorescens*	*Candelariella xanthostigma*	*Collema subflaccidum*	*Diplotomma alboatrum*	*Diplotomma pharcidium*	*Glaucomaria carpinea*	*Huneckia pollinii*	*Lecania naegelii*	*Lecanora argentata*	*Lecanora chlarotera*	*Lecanora saligna*	*Lecidella elaeochroma*	*Lepra albescens*	*Leptogium* cf. *cochleatum*	*Melanohalea exasperata*	*Melanohalea laciniatula*	*Ochrolechia androgyna*	*Ochrolechia arborea*	*Ochrolechia szatalaensis*	*Parmelina pastillifera*	*Parmelina tiliacea*	*Pertusaria pertusa*	*Phaeophyscia nigricans*	*Phaeophyscia orbicularis*	*Physcia adscendens*	*Physcia aipolia*	*Physcia biziana*
LeOm1	L	Oma	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
LeOm2	L	Oma	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
LeOm3	L	Oma	1	1	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
LeOm4	L	Oma	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
LeOm5	L	Oma	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0
LeOm6	L	Oma	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
LeNi1	L	Nia	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
LeNi2	L	Nia	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
LeNi3	L	Nia	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
LeNi4	L	Nia	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
LeIm1	L	Imp	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	0
LeIm2	L	Imp	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0
LeIm3	L	Imp	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
LeIm4	L	Imp	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1
LeIm5	L	Imp	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0
LeIm6	L	Imp	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
LeIm7	L	Imp	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KeGe1	K	Ger	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0
KeGe2	K	Ger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KeGe3	K	Ger	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KeGe4	K	Ger	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
PsRo1	P	Rou	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
PsRo2	P	Rou	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
DiVi1	D	Via	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
DiVi2	D	Via	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DiVi3	D	Via	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0
DiVi4	D	Via	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
DiKa1	D	Kat	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
DiKa2	D	Kat	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
DiKa3	D	Kat	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
ThTh1	T	Thr	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ThTh2	T	Thr	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ThTh3	T	Thr	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ThTh4	T	Thr	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ThTh5	T	Thr	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ThTh6	T	Thr	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Epiphyte type			L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L

Table S5. (*continued*) Raw presence-absence occurrences of lichen and bryophyte species found growing on *Z. abelicea* trees on Crete. Mountain: L: Levka Ori, K: Kedros, P: Psiloritis, D: Dikti, T: Thripti. Site: Oma: Omalos, Nia: Niato, Imp: Impros, Ger: Gerakari, Rou: Rouvas, Via: Viannos, Kat: Katharo, Thr: Thripti. Epiphyte type: L: lichen, M: moss.

Sample / tree ID	Mountain	Site	*Physcia dubia*	*Physcia stellaris*	*Physcia tenella*	*Physconia distorta*	*Physconia enteroxantha*	*Physconia grisea*	*Physconia perisidiosa*	*Physconia subpulverulenta*	*Physconia venusta*	*Pleurosticta acetabulum*	*Polycauliona polycarpa*	*Polyozosia albescens*	*Polyozosia dispersa*	*Polyozosia hagenii*	*Polyozosia populicola*	*Polyozosia semipallida*	*Pseudevernia furfuracea*	*Ramalina farinacea*	*Ramalina fastigiata*	*Ramalina fraxinea*	*Rinodina pyrina*	*Rinodina sophodes*	*Scoliciosporum*	*Tephromela atra*	*Xanthoria parietina*	*Habrodon perpusillus*	*Homalothecium sericeum*	*Leptodon smithii*	*Leucodon sciuroides*	*Nogopterium gracile*	*Orthotrichum affine*	*Orthotrichum lyellii*	*Orthotrichum rupestre*	*Syntrichia laevipila*	*Syntrichia virescens*
LeOm1	L	Oma	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0
LeOm2	L	Oma	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
LeOm3	L	Oma	0	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0
LeOm4	L	Oma	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0
LeOm5	L	Oma	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0
LeOm6	L	Oma	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LeNi1	L	Nia	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
LeNi2	L	Nia	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
LeNi3	L	Nia	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0
LeNi4	L	Nia	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0
LeIm1	L	Imp	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
LeIm2	L	Imp	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
LeIm3	L	Imp	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
LeIm4	L	Imp	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
LeIm5	L	Imp	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
LeIm6	L	Imp	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
LeIm7	L	Imp	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
KeGe1	K	Ger	0	1	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0
KeGe2	K	Ger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1
KeGe3	K	Ger	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0
KeGe4	K	Ger	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
PsRo1	P	Rou	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
PsRo2	P	Rou	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
DiVi1	D	Via	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DiVi2	D	Via	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
DiVi3	D	Via	0	0	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
DiVi4	D	Via	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
DiKa1	D	Kat	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0
DiKa2	D	Kat	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
DiKa3	D	Kat	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh1	T	Thr	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh2	T	Thr	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh3	T	Thr	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh4	T	Thr	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh5	T	Thr	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
ThTh6	T	Thr	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Epiphyte type			L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M	M	M	M	M	M	M	M	M

GENERAL DISCUSSION

The research presented in this thesis helped fill several knowledge gaps related to the effects of browsing and of environmental factors on *Zelkova abelicea* growth. This work also helped better understand patterns of natural recruitment of *Z. abelicea* on Crete, presented for the first time the characteristics of dispersal units, seed sterility and seed weight of *Z. abelicea* and started to investigate a small portion of the poorly studied biodiversity linked with *Z. abelicea*. This thesis revealed that:

1) Browsing by goats is a main limiting factor for the growth of *Z. abelicea* individuals on Crete. When individuals are not browsed anymore, yearly produced shoots measure on average twice the length of those of browsed individuals. Individuals protected from browsing grow more in the first two years after fencing occurred, after which growth decreased, albeit staying higher than in overbrowsed areas. Natural regeneration by seedling establishment is found only in the westernmost populations of *Z. abelicea* on Crete, both in protected and overbrowsed areas, showing that overbrowsing may not be the most important limiting factor to seedling establishment throughout the range of the species. Establishing fenced, protected areas for a few consecutive years is an efficient way to promote *Z. abelicea* regrowth in overbrowsed populations, and allows individuals to reach a sufficient height to escape the appetite of goats, and thus also to produce fruits.

2) Growth in *Z. abelicea*, even when browsing is absent, is not the same everywhere throughout the island. There is a longitudinal gradient in growth rates, with *Z. abelicea* individuals situated in western Crete growing more than those situated further east. Individuals in the easternmost *Z. abelicea* population of Thripti where found to be smaller in size than individuals situated throughout the rest of the range of the species. The variations in *Z. abelicea* growth are mainly explained by climatic patterns throughout Crete. Mainly precipitation quantities in late spring to early summer seem to influence growth.

3) *Zelkova* species possess a unique dispersal unit which is an annually produced shoot that abscices with leaves and fruit in autumn to ensure dispersal. Seed sterility is high amongst *Z. abelicea* individuals and on dispersal units, and strongly variable amongst trees. Proportion of fruits with fertile seeds show strong discrepancies throughout Crete. Trees outside the Levka Ori in western Crete have mostly, oftentimes only, sterile seeds. Fruit weight can be used to distinguish between sterile and fertile seeds, but strongly varies between trees. Fruits with fertile seeds are significantly heavier than those with sterile seeds. Tree size (height, circumference, canopy extension) vary according to geographical position of the trees, and show a longitudinal trend with bigger trees in western Crete and smaller trees further east as well as a positive correlation with fruit soundness.

4) The epiphytic lichen and bryophyte biodiversity associated with *Z. abelicea* is high. Geographical position, tree stature or local topography and browsing intensity all play a role in the composition of the epiphyte community. *Z. abelicea* individuals in western Crete have a higher lichen diversity than elsewhere, whereas individuals in central Crete showed the highest bryophyte diversity. Several previously unknown to Crete or Greece species were recorded, which highlighted the low attention given up to present to epiphytic biodiversity of Cretan trees.

Overall, the different research presented in this thesis highlighted strong geographic differences in *Z. abelicea* shoot growth, seedling presence, seed vitality and weight, tree size and biodiversity. Precise climatic data are difficult to obtain due to the complex Cretan topography, orographic effects and weather patterns and the rarity of weather stations in the mountainous areas of the island. However, most of the differences highlighted above seem to be controlled by local climatic conditions, and in particular precipitation patterns. Precipitation on Crete have a west to east decreasing pattern (Agou et al. 2019, Varouchakis et al. 2018, Vrochidou and Tsanis 2012), and most probably have a strong influence on the growth and regeneration of the species.

Crete is found within the Mediterranean area which has been described as being very susceptible to climate change (Cos et al. 2022, Giorgi 2006, Giorgi & Lionello 2008, Zittis et al. 2022). A decrease in annual as well as seasonal precipitation and increase in annual and seasonal temperatures, coupled with an increase in the frequency and intensity of extreme precipitation or drought events has been taken place in the Mediterranean area during the last decades and these conditions are expected to intensify in the future (Giorgi & Lionello 2008, Natsos & Zerefos 2010, Vogiatzakis et al. 2016, Zittis et al. 2022).

The long-term survival and regeneration of the species over a large part of its natural range as well as the maintenance of its uniquely structured and highly diverse genetics (Christe et al. 2014) are concerning due to the following elements: the above mentioned predicted climatic changes, the current absence of fruit with fertile seeds and seedlings outside of the westernmost mountain range of Crete and the smaller growth and tree size moving eastwards.

However, *Z. abelicea* has shown a high resilience and adaptability during millennia on Crete. Its long-term persistency even under suboptimal conditions, its capacity to easily spread vegetatively and the absence of any recent significant decrease in its distribution range (Kozlowski et al. 2014) may be considered positively for its future survival.

Nevertheless, in the scope of the above-mentioned points, it is important to continue to monitor and study *Z. abelicea,* go on with (long-term) applied conservation actions (e.g. fencing of selected stands) and continue the awareness efforts to promote a more sustainable management and use of the ecosystem in which the species grows.

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There is so much beauty to be found and experienced in those places where the αμπελιτσιε grow. It is difficult to summarize it all in just one paragraph, but Crete is for me the smell of the scented Lamiaceae, of the sea, of dung and grazing animals and of *Z. abelicea* bark. It is the sound of the wind through tree branches, animal bells, falling rocks, shepherds calling their flocks from far away, the unending bumble of hard-working bees that swells into a roar in the afternoon heat, the music and songs of late evenings and the Cretan dialect. It is the hospitability and kindness of the people we met, it is the tentative discussions with shepherds and farmers in the middle of the mountain and the invitations to taste fresh goat cheese in isolated mitata. It is the shadow of griffons and gypaetus high in the sky, the deep blue of the sky (yes it really does have a different tinge), the snow-topped mountains, the swirls of Sahara dust and the ever-changing sea. It is the burn of tsikoudia shared between friends, of xorta, local cheeses, olives and all the delicious culinary specialties of Crete. It is the contrasts between hectic cities and half abandoned sleepy hill-side villages, between mountain and sea. It is the millennia old history and civilization. It is the long hikes up rocky mountain slopes to hidden valleys and abandoned mitata. It is finding fragile seedlings or delicate spring flowers sometimes well-hidden and protected behind spiny plants. It is wondering how many centuries those giant old αμπελιτσιε trees have stood strong and how many more they will see. It is the lunar landscape of the Madara. It is the κατσουνες and the ancient αμπελιτσιε trees with their tiny unknown insects, standing tall, strong and resilient through changes and time. After having worked for so many years with and for the conservation of *Z. abelicea*, I can say that tiny pieces of my heart have remained, intertwined with the branches of *Z. abelicea*, in the Cretan mountains.

I end this section by expressing all my love to my daughter Olivia, this little piece of mischief who entered our lives in the midst of this adventure and who grew alongside my thesis. She has made this piece of work even more spicy, challenging and lengthy, but it was, is and always will be worth every single moment.

CURRICULUM VITAE

Surname: Fazan

First name: Laurence

Date of birth: 04.09.1987

Nationality: Swiss

Education

2017-2022 Doctorate of Science, Department of Biology, University of Fribourg

2011-2014 Master of Science in environmental sciences, Institute of environmental sciences, University of Geneva

2007-2011 Bachelor of Science in Geography, Geography Unit, Department of Geosciences, University of Fribourg

2003-2006 Maturité Gymnasiale, Lycée Jean-Piaget, Neuchâtel

Work experience

2022-present Scientific collaborator, Domaine environnement et durabilité de la Défense, Etat-major de l'armée, Département fédéral de la défense, de la protection de la population et des sports

2021-present Scientific collaborator, Botanic garden of the University of Fribourg

2017-2022 Graduate assistant, Department of Biology, University of Fribourg

2015-2017 Junior researcher, Department of Biology, University of Fribourg

2013-2014 Scientific assistant, Department of Biology, University of Fribourg

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