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The role of olive groves in the conservation of Mediterranean orchids

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ABSTRACT

Olive and olive oil production is one of the main agricultural activities in the Mediterranean region. Besides their economic importance, traditional and organic olive groves were also hypothesized to contribute to biodiversity conservation. For instance, the presence of terrestrial orchids in olive groves has long been known. It is, however, not well understood what ecological or biological traits of olive groves influence the species richness and abundance of these protected flora elements in these secondary habitats. We surveyed 273 olive groves across the mainland of three countries (France, Greece, Italy) and three islands under their administration (Corsica, Lesbos, Sardinia). The surveyed olive groves provided habitat to more than 60,000 orchid individuals belonging to 45 species. Our results indicate that olive groves located on islands had a significantly greater potential for orchid conservation, as they harbored more species and individuals than olive groves on the mainland. Furthermore, orchid presence and species richness was highest in olive groves located on islands with high diversity of pasture weeds or native woody species, while these results also highlight the more traditional use of island groves and a difference in the intensity of maintenance between island and mainland groves. Overall, our study suggests that Mediterranean olive groves contribute significantly to the conservation of diverse terrestrial orchid communities and highlights the importance of traditional management practices in olive groves that allow local biodiversity to flourish.

1. Introduction

Recent developments in agricultural practices (e.g. the use of machines, use of chemicals, the dominance of large monocultures) and the expansion of human populations has led to the drastic decline of natural and undisturbed habitats worldwide. This resulted in an ongoing biodiversity crisis (Singh, 2002; Zabel et al., 2019) with once ubiquitous flora and fauna elements declining in abundance, distribution, health and diversity. While the overwhelming majority of human activities cause damage, some (often unintentionally)

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create habitat patches that despite their disturbed nature provide refuge to important or rare organisms. These habitats are called secondary or anthropogenic habitats and include (among others) kurgans (Deák et al., 2016), cemeteries (Molnár et al., 2017a; Löki et al., 2019), roadside verges (Fekete et al., 2019, 2020) or plantations (Molnár et al., 2022; Süveges et al., 2022) and they often play prominent roles in maintaining local biodiversity (e,g, Kowarik et al., 2016; Valkó et al., 2018; Jakobsson et al., 2018). Anthropogenic forest groves mainly include monocultures of cultivated tree species of commercial or agricultural importance, such as trees used in timber or food production (e.g. orchards, poplar plantations, etc.). Such monocultures include also olive groves, which are abundant in southern Europe and have been shaping the Mediterranean landscape for millennia (Loumou and Giourga, 2003). Due to their economic profit and their adaptation to local climate, olive groves are expected to become even more widespread in this region in the future (Gambella et al., 2021).

Olive trees (*Olea europaea*) are likely the earliest cultivated woody plants of Southern-Europe (Liphschitz et al., 1991). Currently there are two known variants: (1) *Olea europaea* var. *sylvatica* and (2) *Olea europaea* var. *europaea*. The former is widespread surrounding the Mediterranean Sea and occurs in natural woody plant communities (Gianguzzi and Bazan, 2019), while the latter is mostly cultivated, thus generally occurs in large numbers and has more than 1000 variants worldwide (Bartolini et al., 1993; Kapellakis et al., 2008). Olive trees are one of the longest living extant flowering plant species known today, with some individuals being estimated to be over 1000 years old (Ninot et al., 2018). They are long-lived, well adapted and native to the Mediterranean and their understory likely facilitates the maintenance of native vegetation.

The most important product of olive trees is olive oil and the majority (ca. 67 %) of worldwide olive oil production comes from the European Union (European Commission, 2020). The three largest olive oil producing countries in the world, in order, are Spain, Greece and Italy (European Commission, 2020). It is thus no surprise that a significant part of land in the European Mediterranean region (ca. four million hectares) are occupied by olive groves (Infante-Amate, 2012; Marchi et al., 2018; Cecchini et al., 2019; European Commission, 2020). Olive groves can be grouped into two main categories based on their management practices: (1) intensively managed conventional olive groves and (2) extensively managed traditional (mostly organic) olive groves. The broad objective of conventional farming is to increase production and profit using intensive monocultures and treatments, such as the use of pesticides (Amvrazi and Albanis, 2009), herbicides (Sánchez-Moreno et al., 2015) fertilizers (Kampoyrakis, 2004) and irrigation (Campos-Herrera et al., 2022). In contrast, extensive olive groves are often managed at a low intensity, with limited or no irrigation and chemical input which can also contribute to biodiversity (The Soil Association, 2000). This is also well reflected by the biodiversity of olive groves, as conventional olive groves are characterized by lower bird, bat and herbaceous plant diversity (Solomou and Sfougaris, 2011; Morgado et al., 2020; Herrera et al., 2015; Jiménez-Navarro et al., 2023), as well as by poorer soil health (Sánchez-Moreno et al., 2015) than traditionally managed ones. Traditional olive groves are typically used as pastureland for livestock, which has been providing livelihood for people in the region for centuries (Sternberg et al., 2000).

There are two main, conflicting effects of livestock grazing in Mediterranean ecosystems. On the one hand, grazing and stomping by livestock can be beneficial by creating disturbed, bare patches of ground that can serve as ideal habitats for pioneer or partly pioneer plant species, for instance, various species of European orchids (Gardiner and Vaughan, 2009). On the other hand, overgrazing can be exceptionally harmful in these habitats, due to the higher risk of flower and fruit herbivory and higher intensity of trampling of plants (Paton et al., 1997), and can harm orchids as well (Molnár et al., 2017a). The Mediterranean region is generally considered a biodiversity hotspot for orchids, providing home to the highest diversity of orchid species across all Europe (e.g. Vereecken et al., 2010; Delforge, 2006). However, a large proportion of formerly natural orchid habitats has been cultivated, often being transformed into secondary and/or semi-natural habitats. Besides habitat loss and/or disturbance, global climate change exerts additional unfavorable pressure on orchid habitats (Barredo et al., 2016). Despite these unfavorable changes, many orchid species thrive in the Mediterranean, often occupying secondary habitats (Schönfelder and Schönfelder, 1984; Kretzschmar et al., 2004; Delforge, 2006). Such secondary habitats include Mediterranean olive groves, especially those situated within Europe, which can provide habitats for significant orchid populations (Kreutz, 1998; Delforge, 2006; Petanidou et al., 2013). While this has been a widely known phenomenon among orchid experts of Europe, only a few floristic reports and observations mention occasional occurrences of orchids in olive groves (e.g. Vuković et al., 2011; Croce and Nazzaro, 2012; Perrino and Calabrese, 2014; Molnár et al., 2017b; Bódis et al., 2018; Tsiftsis and Tsiripidis, 2020; Solomou and Sfougaris, 2021).

Other factors, like geographic latitude and altitude could also influence orchid diversity in olive groves. Several studies have found that the distributional pattern of orchids follows a latitudinal diversity gradient (LDG) (Vakhrameeva et al., 2008; Bjørndalen, 2015; Zheleznaya, 2015), where species richness negatively correlates with latitude (MacArthur, 1972). Accordingly, in Europe it is the Mediterranean region, which harbors the highest number of orchid species (Hágsater and Dumont, 1996). Moreover, altitude can similarly affect orchid diversity, since higher altitudes are characterized by lower temperature and greater seasonality. The effect of growing altitude on orchid species richness usually shows a unimodal curve (Bhattarai and Vetaas, 2003; Tsiftsis et al., 2019). In this study we aim to fill this gap by investigating the occurrence patterns of orchids in Mediterranean olive groves, as well as the factors (e.g. olive grove characteristics) influencing these patterns. More specifically we investigate: i) the richness and abundance of orchid species in Mediterranean olive groves, ii) whether there are regional differences in orchid occurrence in olive groves, and iii) which olive grove characteristics influence the suitability of these to orchids (e.g. area, altitude, island/mainland status, plantation age, grazing activity, understory type and understory plant species composition).

2. Materials and methods

2.1. Field surveys

Field surveys were conducted during 2018–2019 in mainland Greece, Italy and France, as well as on three large islands under the administration of these countries: Lesbos, Sardinia, and Corsica. During the surveys, we visited a total of 273 olive groves that were randomly spotted along roads while driving. Our only selection criterion was to avoid plantations that were recently ploughed (1–2 years ago) due to the poor vegetation that generally characterize them. In each surveyed olive grove, we recorded geo-coordinates and the altitude using a handheld GPS device. We carefully surveyed the plantations, covering the entire area and recorded the detected orchid species, as well as the orchid individual abundance of each species (Table S1). When orchids were not overly abundant, we counted the number of specimens, while in case of large population sizes (e.g. hundreds or thousands of individuals) orchid individual abundance was estimated by extrapolating the counted number of individuals in one square meter to the total area covered with individuals. Orchid species identification was carried out following Delforge (2006). To characterize the density of the olive groves, we measured the distance between ten randomly selected olive trees and the tree in their closest proximity in each plantation. To characterize the age of olive groves we additionally measured the trunk diameter (at 150 cm height) of ten randomly selected olive trees (Table S2). Given that larger plantations might provide habitat for more orchid species and individuals, following fieldwork, we also measured the total area of each surveyed olive grove using satellite images provided by the Google Earth Pro software (matching the year of the survey of each plantation).

In order to characterize the local biodiversity, we recorded the number of species and specimens of the native woody species and pasture weeds in each surveyed plantation along a randomly designated, 50 m long straight transect. In some cases, when neither dimension of the olive grove reached 50 m, we surveyed the grove along its longest diagonal. We recorded the following native woody species: (1) shrubs (e.g. *Lavandula* spp., *Cistus* spp.), (2) chamaephytes (e.g. *Thymus* spp., *Phlomis* spp.), (3) smaller trees and their seedling (e.g. *Quercus* spp., *Pistacia* spp. *Pyrus nivalis*). We also recorded pasture weeds: prickly (e.g. *Cirsium* spp., *Carduus* spp., *Eryngium* spp.), poisonous plant species (e.g. *Asphodelus* spp., *Dracunculus vulgaris*), and blackberries (*Rubus* spp). In some cases, identification was only possible to the genus or family level (Table S3). Information on native plant species was used to calculate Shannon diversity indices of native woody species and pasture weeds for each olive grove.

2.2. Data analyses

To explore the effect of olive grove characteristics on orchid presence, abundance and species richness we constructed generalized linear mixed models (GLMMs), with the following dependent variables respectively: (1) the presence or absence of any orchid species (GLMM with binomial error distribution), (2) species richness, and (3) orchid individual abundance, irrespective of species (for models 2 and 3, a GLMM with quasipoisson error distribution was used due to significant overdispersion in this parameter). All GLMMs included the following explanatory variables: (1) altitude, (2) average trunk diameter of olive trees in the grove, (3) average distance between olive trees in the grove, (4) Shannon diversity of pasture weeds (5) Shannon diversity of native woody species in the grove (6) total area of the grove, (7) latitude (8) location of the grove, whether it was located on an island or on the continent and (9) country and (10) the interaction of country and island to test the degree of difference between island and mainland regarding orchid presence, species richness and individual abundance.

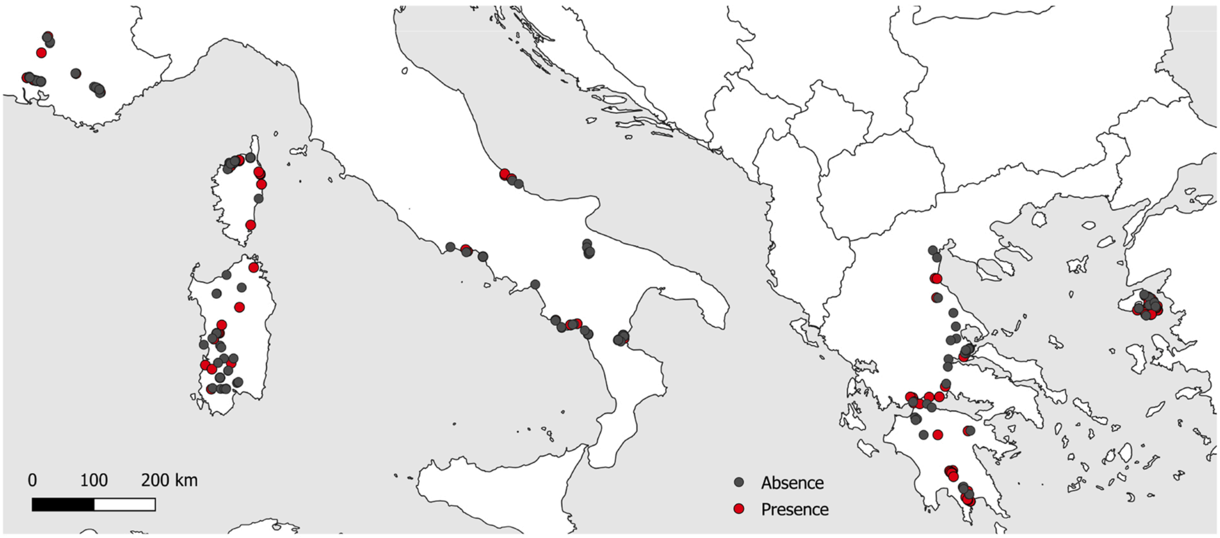

Fig. 1. The location of the surveyed olive groves. Groves with orchid presence or absence are indicated with red and gray dots, respectively.

To test whether there is difference between olive groves located on islands and mainland in the measured environmental variables (altitude, Shannon diversity of native woody species, Shannon diversity of pasture weeds, distance between trees trunk diameter, latitude and total area of the olive grove) we built six LMM-s. In these LMMs we used the mentioned environmental variables as dependent variables in separate models and the interaction between island and country as a predictor. When the interaction was not significant, we removed it from the model.

When analyzing orchid presence, abundance and species richness, we started by building full models containing all explanatory variables. This was followed by model simplification: non-significant predictors were removed from the models using a backward stepwise procedure (based on the largest p-values) until minimally adequate models were obtained (containing only variables with a statistically significant effects: $p < 0.05$). All statistical analyses were carried out using the R statistical and programming environment, version: 4.2.1 (R Core Team, 2021). Mixed models were built as implemented in R package *lme4* (Bates, 2010). Overdispersion in GLMMs was tested using dispersiontest function in R package *AER* (Kleiber and Zeileis, 2008) Anova was used to obtain analyses of deviance tables.

3. Results

3.1. General results

We documented a total of 61,424 orchid individuals belonging to seven genera and 47 orchid species in the surveyed 273 olive groves (Table S4). More than half (52.7 %) of the surveyed olive groves harbored at least one orchid specimen (Fig. 1).

The number of orchid species in a single olive grove varied from zero to a maximum of ten taxa, while the detected number of orchid specimens varied from one to an estimated 35,561 individuals. The three groves that contained the largest number of specimens were all found on the island of Lesbos (with 35,561, 6151, and 2220 individuals, respectively). Overall, the highest average species richness per area in olive groves was documented on Lesbos (0.60 species/ha), while the lowest average species richness was found in Corsica (0.25 species/ha) (Table 1).

The most common orchid species in olive groves were *Serapias parviflora* (55 groves, 20.15 %), *Anacamptis sancta* (35 groves, 12.82 %) and *Anacamptis papilionacea* (26 groves, 9.52 %). We also detected some rare, endemic taxa such as *Anacamptis boryi* (one grove), *Ophrys pollinensis* (one grove), *Ophrys spruneri* (five groves). We could only identify the genus due to the phenological state in case of one *Ophrys* individual.

3.2. Factors determining orchid occurrence patterns in olive groves

Shannon diversity of native woody species and Shannon diversity of pasture weeds had a significant positive effect on orchid presence in olive groves (Table 2, Fig. 2). Latitude and trunk diameter had a significant negative effect on orchid presence. Interaction of country and island also significantly affected orchid presence. Difference in probability of orchid presence between islands and mainland was significantly higher in case of Lesbos and Greece mainland than in case of the other islands and countries (Fig. 3). Distance between trees, altitude and the area of the olive groves did not influence significantly the presence of orchids (Table S5).

The models indicated that geographic altitude had a significant positive effect, while latitude had a significant negative effect on species richness, (Fig. 4). Difference in the number of species between islands and mainland was significantly lower in case of Italy mainland and Sardinia than in case of the other islands and countries regarding the number of orchid species (Fig. 5, Table 3). Shannon diversity of pasture weeds or native woody species, distance between trees, trunk diameter and the area of the olive grove did not have significant effects on species richness (Table S5). None of the surveyed variables have a significant effect on orchid individual abundance.

LMMs showed that there was no significant difference between island and mainland groves in the Shannon diversity of native woody species, but the Shannon diversity of pasture weeds, the distance between trees and the area of the olive grove was significantly higher on islands than on the mainland (Table S6). Altitude of olive groves and tree trunk diameter was significantly lower on islands than on the mainland, while our sampling points on islands were located at significantly lower latitudes than those on the mainland (Table S6).

Table 1
Summary of the number of documented orchid species and individuals and the average number of species and individuals per area (ha) in the surveyed olive groves.

Country	Region	Year	Number of surveyed groves	Number of species	Total number of individuals	Average number of species/ha	Average number of individuals/ha
Greece	Lesbos	2018	51	21	50,154	0.60	1423.61
Greece	Mainland	2019	62	21	4333	0.51	104.33
Italy	Sardinia	2019	40	11	508	0.38	17.53
Italy	Mainland	2019	50	14	2930	0.30	63.11
France	Corsica	2019	30	9	2600	0.25	73.09

Table 2
Results of the model predicting orchid presence.

	LR Chisq	Df	p value
Country	10.9920	2	0.004
Island	5.5627	1	0.018
Trunk diameter	4.6320	1	0.031
Latitude	4.6244	1	0.032
Shannon diversity of pasture weeds	7.0783	1	0.008
Shannon diversity of native woody species	16.2438	1	< 0.001

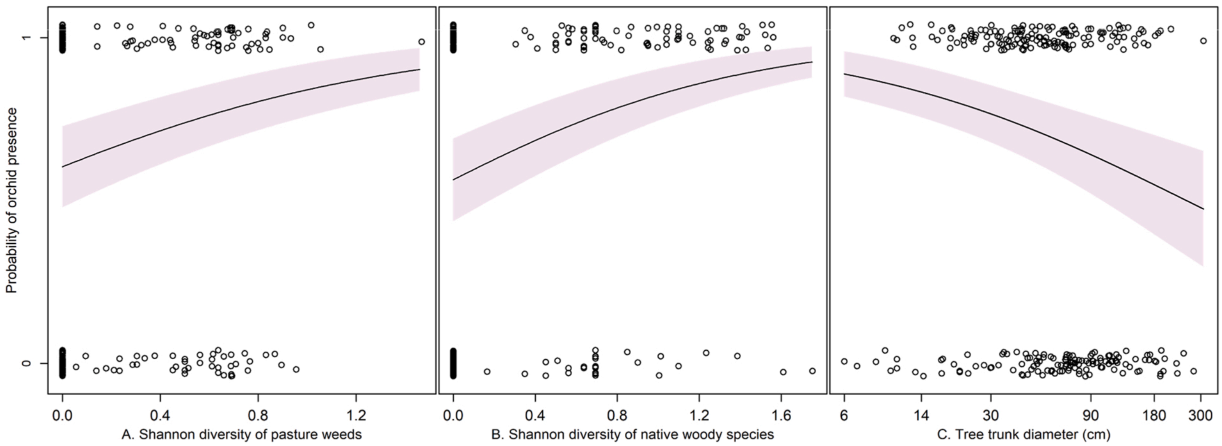

Fig. 2. Probability of orchid presence in function of the Shannon diversity of pasture weeds (A) native woody species (B) and Tree trunk diameter (C).

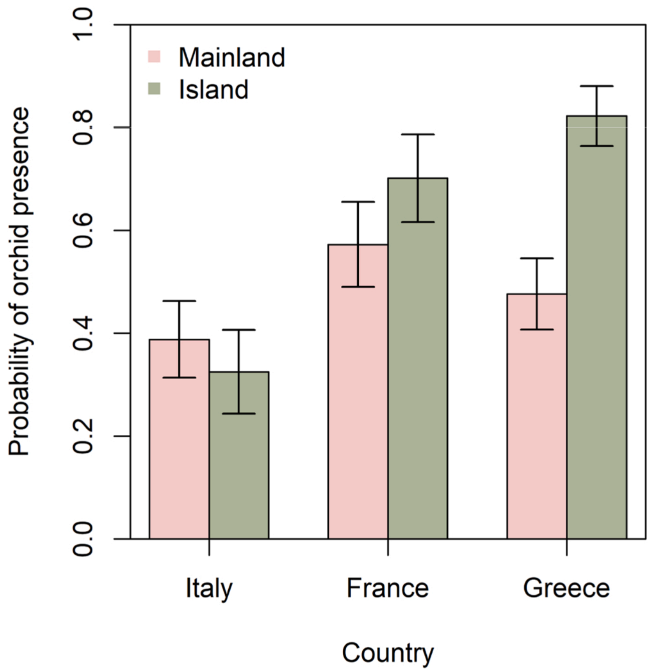

Fig. 3. Probability of presence on islands and mainland of the three surveyed countries.

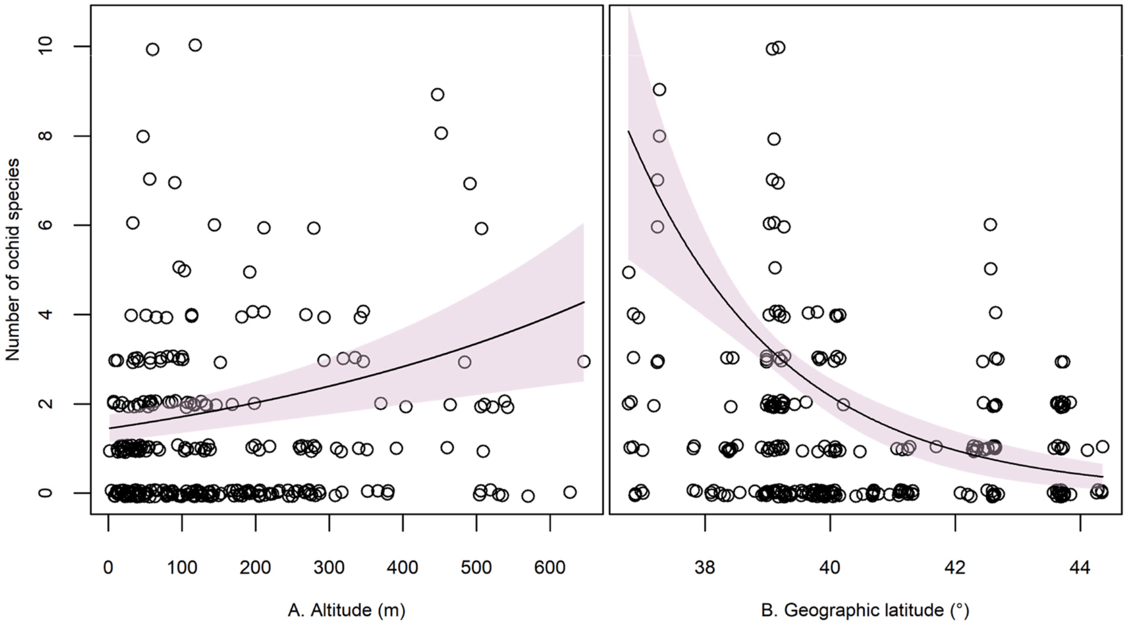

Fig. 4. Species richness in function of A. altitude and B. Geographic latitude.

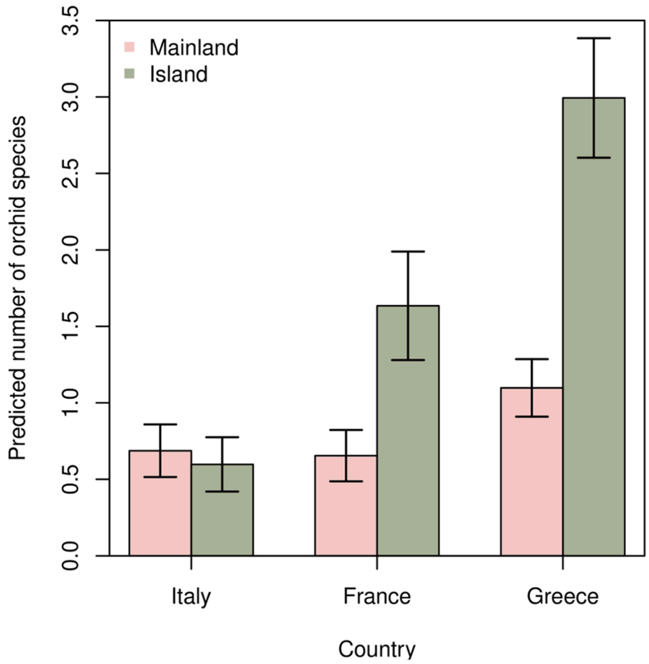

Fig. 5. Number of orchid species on islands and mainland of the three surveyed countries.

Table 3
Result of the model exploring variation in the number of orchid species in olive groves.

	LR Chisq	Df	p value
Country	30.9438	2	< 0.001
Island	19.9734	1	< 0.001
Altitude	8.1625	1	0.004
Latitude	8.4004	1	0.004

4. Discussion

In this study, we investigated ecological and biological factors affecting orchid presence, species richness and abundance in olive groves of the Mediterranean region. Our field surveys indicate that half of the visited Mediterranean olive groves harbored orchids with more than 60,000 individuals altogether in the visited regions. Our statistical analyses showed that grazed olive groves provided more favorable conditions to terrestrial orchids than non-grazed ones probably due to more open vegetation caused by grazing. Additionally, we have shown that olive groves with diverse native woody vegetation are the most favored olive groves habitats by terrestrial orchids. Both of the latter results emphasize the importance of extensive, traditional land use practices in olive production. Moreover, we showed that olive groves located on islands harbored higher abundance and species richness of orchids than those situated on the mainland, especially in France and Greece.

We found an overall difference between island and mainland groves regarding orchid presence and species richness. Our results also highlighted the more traditional use of island groves and a difference in the intensity of maintenance between island and mainland groves since the Shannon diversity of pasture weeds, the distance between trees and the area of groves were all higher or larger on islands. However, we did not find any effect of area and the distance between trees on orchid presence, species richness or abundance, we assume that these are characteristics of a more extensive use of olive groves. Other studies also highlighted the effect of the intensification in olive cultivation on biodiversity and orchid flora of groves (Tsiftsis and Tsiripidis, 2020). The latter study highlighted the importance of slope characteristics and elevation on the composition of vegetation, with groves on steeper slopes and at higher altitudes being characterized by more traditional maintenance practices (Allen et al., 2006).

Other factors associated with biogeography could also influence orchid diversity. For example, diversity of orchids on continental islands can reach remarkably high levels (Taylor et al., 2019), thus our results in connection with a higher orchid species richness on island groves is in line with this. Furthermore, some other biotic and abiotic factors, such as larger island area, temperature or forest cover could also increase orchid diversity on islands (Taylor et al., 2021).

In the sampled olive groves, geographic altitude had a significant positive effect on the number of orchid species. Similar results have been found in the case of other anthropogenic habitats, such as cemeteries (Löki et al., 2015). This phenomenon might be explained by the natural distribution range of orchids, which often tend to prefer higher altitudes or it could be explained by the peculiar microclimatic conditions of higher altitudes in the Mediterranean region (Bertolini et al., 2012). Alternatively, olive groves at higher altitudes could be under less intensive management (because of e.g. steep terrain conditions). Furthermore, it has been shown that orchid species richness generally shows a unimodal curve with increasing geographic altitude with higher species richness in mid elevations (Grytnes, 2003; Bruun et al., 2006), which means a growing plant species richness until 1500 m above sea level (asl) (Grytnes and Vetaas, 2002). The olive groves surveyed by us were all much below 1500 m asl, hence the observed positive trend between species richness and growing altitude.

Geographic latitude was also an important predictor of orchid presence and species richness showing a trend of increasing species richness towards the south. Well-known hypotheses, like the latitudinal diversity gradient (LDG) have long been described the growing species richness with decreasing latitude (MacArthur, 1972), but recent studies also confirm this phenomenon (Hillebrand, 2004; Tsiftsis et al., 2019). Tsiftsis et al. (2019) found that species richness of tuberous orchids is growing, while species richness of rhizomatous and intermediate species is decreasing with decreasing latitude. This finding is in line with our results since all of the orchids found during the study were tuberous, Mediterranean species. Additionally, the islands surveyed within the framework of this study are situated at significantly lower latitudes than the surveyed mainland areas, which could also explain the greater diversity and abundance of orchids in island groves.

Based on earlier studies, which found a linear relationship between trunk diameter and age of olive trees (Arnan et al., 2012; Camarero et al., 2021), we assumed that larger and older trees are characteristic to a more extensive use of groves. Contrarily, we found a negative effect of trunk diameter on the probability of orchid presence. There might be several reasons that lie behind these results, such as confounding effects, including water and salinity levels which could also affect the growth of olive trees (Aragüés et al., 2004). Alternatively, the high light requirement of Mediterranean orchids (Delforge, 2006) can explain this association, indicating that larger canopy cover provides suboptimal conditions for these orchids.

We found that Shannon diversity of pasture weeds had a significant positive effect on the probability of orchid presence in olive groves. Based on results of other studies and together with our findings, it seems that a moderate level of grazing is favorable for orchids. Livestock are capable of keeping the vegetation low, slowing down succession by their grazing and trampling, preserving orchid habitats. The positive effect of grazing on the presence of orchids is well-known in the scientific literature: a continuous, low level of grazing does not cause a decrease in orchid populations according to a study carried out on a dry calcareous grassland (Köhler et al., 2016). In the case of the early spider-orchid (*Ophrys sphegodes*), it has been found that grazing can facilitate the conservation of the habitat and can even cause an increase in species abundance, but only if the grazing period does not overlap with blooming and ripening of orchids (Hutchings, 2010). On the other hand, overgrazing can be especially harmful, firstly because orchids are edible for livestock, and secondly because intensive grazing can significantly alter the habitat, as well as its phytocoenological and soil conditions, resulting in the decrease of orchid abundance and species richness (e.g. Evans et al., 2015; Kairis et al., 2015). Overall, our study emphasizes the importance of moderate intensity grazing, the way dictated by traditional management practices which appears to have facilitated the maintenance of the Mediterranean ecosystem as a biodiversity hotspot throughout centuries (Sirami et al., 2010).

The Shannon diversity of native woody species positively correlated with the presence of orchids in the surveyed olive groves. The presence of these woody species is likely also a result of extensive farming and the lack of intensive soil disturbance (e.g. ploughing). Olive groves inhabited by such woody species generally presented a more natural landscape, forming a semi-open habitat. Olive groves with shrubs in the understory can have a cooler microclimate and soil that is more protected from erosion (Juhren, 1966), all of which can have a positive effect on orchids. According to a study conducted in the Mediterranean-like parts of Chile, there were significantly more orchid individuals under native shrubs than in open habitats, probably due to reduced herbivory (Atala et al., 2020). Similar results have been found by Kelemen et al. (2017) in Hungary, demonstrating the protective effect of native shrubs on herbaceous species (including orchids) found in their proximity. On the other hand, olive groves that are not covered by undergrowth have a significantly reduced soil flora and fauna, as well as a less intensive circulation of nutrients compared to olive groves that have vegetation cover (Gkisakis et al., 2014; Sánchez-Moreno et al., 2015). Similarly, in our study, the presence of native woody species in olive groves – implying significant undergrowth – had higher orchid abundance and species richness compared to olive groves that were ploughed. The role of understory and extensive management practices in maintaining biodiversity in olive groves was also supported by an eight-year long experiment, showing that olive groves that had a secondary use of hay production had larger biodiversity and better water retaining capacity, while olive production remained unchanged (Simoes et al., 2014). It is generally well documented that organic farming has a positive effect on soil quality and biodiversity. These studies and our results indicate that the beneficial effects of extensive management practices and organic farming are also detectable in the case of olive groves (Calabrese et al., 2015).

5. Conclusion

Our study revealed the role of olive groves in the conservation of Mediterranean orchid and highlighted the importance of maintenance practices. We found that different abiotic or biotic factors could have a significant effect on orchid presence and species richness in olive groves. We highlighted the role of traditional management practices, which is associated with native woody species, pasture weeds and higher altitudes. We further found a more important role of island olive groves in the preservation of orchids, also associated with extensive land use. Surveying more olive groves in other Mediterranean areas (e.g. Spain) and testing other variables such as slope aspect and angle could improve our knowledge of the role of olive groves in orchid conservation.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02490.

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