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Plants in danger: Floral and other plant traits as drivers of vulnerability in Mediterranean countries

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ABSTRACT

Plants with complex floral morphologies are adapted to be pollinated by restricted pollinator assemblages and may suffer pollinator limitation. Understanding how floral traits and other variables relate to plant vulnerability can provide a powerful tool for predicting the conservation status and prioritizing the assessment of plants with scarce field data. Using circa 3000 records of rare and threatened (sensu IUCN) entomophilous plant taxa from seven Mediterranean countries, we evaluated how six floral traits and other eight intrinsic and extrinsic variables were related to plant vulnerability (less vs. more threatened plants). Besides, we analyzed 29 experts' opinions regarding the floral traits most related to floral complexity. Floral shape, reproductive unit, and flowering duration were good vulnerability indicators. Taxa with lip- and flag-shaped flowers were the most threatened, which agrees with the opinion of experts who considered lip- and flag-shaped flowers to have more complex morphologies. Also, plants with cylindrical inflorescences or solitary flowers were more threatened than those with flat-spherical inflorescences; and longer flowering durations reduced the probability of being threatened. Regarding extrinsic variables, coastal and freshwater habitats, i.e. habitats heavily impacted by human activities, had the highest percentage of highly threatened taxa. Yet, plant vulnerability decreased with maximum elevation and total distribution range. These results may serve as a basis for managers and practitioners when field data are

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scarce or unavailable, so that, depending on their traits, species could be provisionally listed in Red Lists as deserving priority for assessment to ascertain conservation status and actions.

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1. Introduction

Pollination comprises a basic step for the sexual reproduction of plants and, thus, constitutes a fundamental process for maintaining ecosystem diversity and functioning (Potts et al., 2010). Most flowering plants (estimated to be 87.5 % or 308,006 species) depend on pollinators for reproduction (Ollerton et al., 2011). This implies that plants that fail to attract effective pollinators may be more prone to extinction (or local extirpations) due to the negative effects of pollination failure on their reproduction (Fontaine et al., 2006; Lundgren et al., 2013) and recruitment (Lundgren et al., 2016). This problem has become particularly evident in the last decades, as global pollinator declines (Biesmeijer et al., 2006; Potts et al., 2010; Burkle et al., 2013) are directly associated with the loss of flowering plants (Biesmeijer et al., 2006; Lundgren et al., 2016).

Floral traits not only function as attractive features for pollinators (Fægri and van der Pijl, 1966; Chittka and Thomson, 2001), but also determine the level and accessibility to rewards (Lázaro et al., 2015; Stang et al., 2006, 2009), promote cross-pollination by increasing pollen placement precision on the pollinator's body (Neal et al., 1998; Citerne et al., 2010), and enhance the fidelity of more efficient pollinators (Campbell et al., 1996; Rodríguez-Gironés and Santamaría, 2004). Complex and specialised floral morphologies (i.e. those with a set of floral characteristics that restrict the number of efficient pollinators) have evolved through strong selection exerted by a small set of animals (Nilsson, 1988; Neal et al., 1998). Consequently, these morphologies are, in general, associated with a more restricted pollinator assemblage, mainly specialised pollinators that are more at risk (Biesmeijer et al., 2006), whereas less complex morphologies are associated with visitation by a wide spectrum of pollinators (Fenster et al., 2004; Lázaro et al., 2008; Watts et al., 2016; Yoder et al., 2020; Bergamo et al., 2021). For this reason, plants with complex and specialised floral morphologies are expected to be more vulnerable than others due to pollination failures. Based on this idea, a previous study using the Greek Red Data Book (Stefanaki et al., 2015) showed that plant vulnerability was positively related to floral symmetry and floral complexity (i.e., estimated using Floral Complexity Index – FCI, an index that included floral shape, symmetry, depth, corolla segmentation, and functional reproductive unit). In addition to floral complexity, other traits may also be related to pollinator generalization and in turn to reduced vulnerability. For instance, floral colour might influence the diversity of pollinators of plant species; indeed, several studies have reported higher generalization in yellow and white flowers compared to other colours such as purple, lilac, blue or red (Lázaro et al., 2008; Bergamo et al., 2021). Pollinator generalization may also be higher in species with larger pollination units (Lázaro et al., 2008, 2020; but see Bergamo et al., 2021), because overall pollinator visitation increases with floral size (Bell, 1985; Eckhart, 1991). Similarly, pollinator visitation (Høye et al., 2013) and generalization (Lázaro et al., 2020) may increase with flowering duration, as the longer flowers remain available to pollinators, the higher their probability of being visited. Indeed, a study on the Czech flora (Gabrielová et al., 2013) showed that Critically Endangered plants had shorter flowering periods than other species. Lastly, other plant traits might also influence vulnerability, such as flowering season, which could affect pollinator availability (Rafferty and Ives, 2010; Petanidou et al., 2014), or species' life form that will determine the habit and life span of species and therefore their reproductive strategy (Lovett Doust and Lovett Doust, 1988).

The above studies suggest that plant traits, particularly floral traits that are recognizable at first glance, should be considered in plant conservation schemes. However, the protocols established by the International Union for the Conservation of Nature (IUCN) to assess plant conservation status focus primarily on population sizes and declines, geographic ranges and quantitative extinction probability analyses (IUCN, 2024), without considering in any case plant traits directly related to pollination. It can be argued that if in a known flora the most threatened plants (as included in a given Red List) are those with particular floral or plant traits, then, in an unexplored flora (of which field data are unavailable or inadequate) it might be possible to identify the plants that are more likely to be threatened based on these characteristics. This may constitute a tool for pre-assessing plant species for which field data are unavailable; these taxa could be preliminarily red-listed as deserving priority for more profound studies to ascertain conservation status and actions. The same applies to other extrinsic variables that are not part of the IUCN criteria but are usually reported in the Red Data Books as additional attributes (e.g. habitat, elevation or distribution range) and may also act as reliable predictors of plant vulnerability (Bacchetta et al., 2012; Stefanaki et al., 2015).

The Mediterranean Basin is one of the world's biodiversity hotspots (Myers et al., 2000; Cañadas et al., 2014), where, in an area covering only 1.6 % of the Earth's surface (Médail and Quézel, 1997), ca. 10 % of the world's higher plant species can be found, including 5500 narrow endemics (Médail and Quézel, 1999). By using data on ca. 3000 records of threatened animal-pollinated plant taxa from seven Mediterranean countries (Portugal, Spain, southern France, Italy, Greece, Cyprus, and Lebanon), we evaluated whether certain floral traits as well as other plant characteristics and extrinsic variables can predict plant vulnerability; and whether floral traits more related to plant vulnerability coincided with those considered as the most complex by pollination experts. Specifically, we addressed the following questions: (1) to what extent do floral traits (shape, colour, depth, symmetry, size, and functional reproductive unit) and other plant traits (flowering duration, flowering season, and life form) influence plant vulnerability? (2) To what extent do extrinsic variables such as habitat, elevation, and total distribution influence plant vulnerability? (3) Does the opinion of world pollination experts regarding the complexity of certain floral traits differ from our results? By answering these questions, we aim to aid plant conservation policies by highlighting certain traits that trigger plant vulnerability but are not currently considered in conservation assessments.

2. Methods

2.1. Study taxa

The data set used here comprises plant taxa from seven countries of the northern Mediterranean region (including their islands; Fig. 1): Portugal, Spain, meridional France (southern half of the country and Corsica), Italy, Greece, Cyprus, and Lebanon. Initial datasets of the entomophilous flora listed in the national Red Data Books were compiled for each country (wind- and water-pollinated taxa excluded; references to Red Data books in Appendix S1). We focused on 49 plant families (see the families and the number of taxa per family and country in Table S2.1 in Appendix S2). These plant families represented 86 % of the threatened entomophilous taxa in the above-mentioned Mediterranean countries and were selected because they included a large variety of floral shapes and other intrinsic and extrinsic characteristics. The nomenclature was updated according to Plants of the World Online (POWO, 2024), and species and subspecies were carefully revised, considering synonyms and excluding nomenclaturally outdated or duplicated records. Since not all Mediterranean countries examined here had assessed their entire flora using IUCN criteria and to standardize all datasets, taxa considered as "Least Concern (LC)" were removed from the analysis, as this group was underrepresented in many countries' datasets. After the data cleaning process, we included in our analyses 2959 records of 2773 different entomophilous threatened plant taxa (study taxa, hereafter). The number of taxa per country (Fig. 1) varied between 73 (Lebanon) and 925 (Spain).

2.2. *Plant vulnerability*

Plant vulnerability was determined by using each taxon's IUCN conservation status given in the National Red Data Books and other related literature (Appendix S1). Following Stefanaki et al. (2015), these categories were aggregated into two groups: (1) Less threatened, including Vulnerable (VU), Near Threatened (NT) and Rare (R) taxa; and (2) More threatened, including Endangered (EN), Critically Endangered (CR), Regionally Extinct (RE), Extinct in the wild (EW), and Extinct (EX) taxa.

2.3. *Variables potentially related to plant vulnerability*

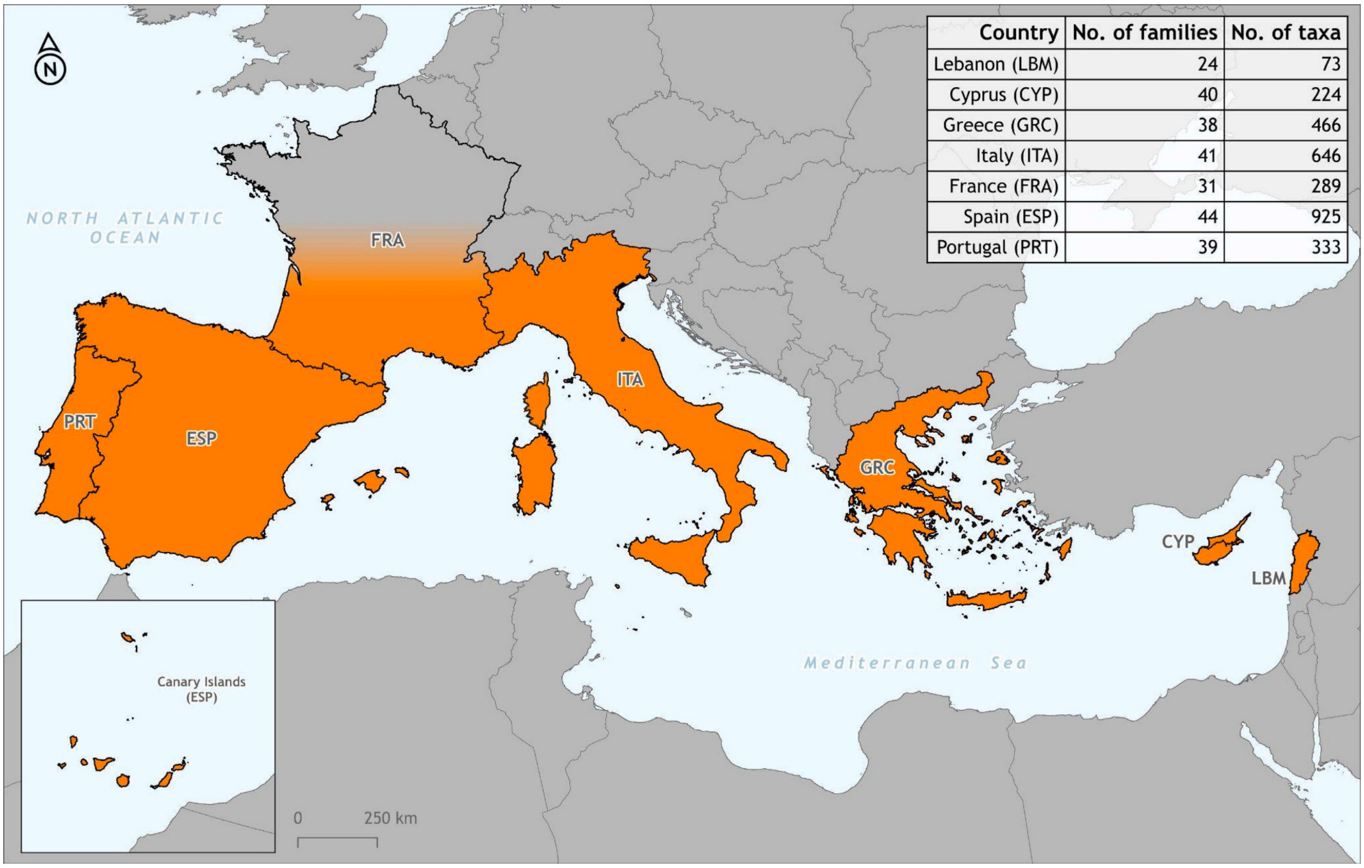
We assessed 15 intrinsic and extrinsic variables potentially related to plant vulnerability (Stefanaki et al., 2015) for all study taxa across the Mediterranean countries studied. To estimate these variables, we retrieved information from a wide range of published literature, the countries' Red Data Books and Red Atlases, major floras, online herbarium collections, original descriptions of taxa and other taxonomic and floristic papers, books and online databases (see references for all the compiled information in Appendix S1). All the variables associated with the study taxa were calculated and revised by at least two independent researchers (within the co-authors).

2.3.1. *Floral traits related to floral complexity*

The following four floral traits related to floral complexity were assigned to each taxon:

Floral shape – Flowers were assigned to one of the following 11 functional floral shapes (Fægri and van der Pijl, 1966; Barth, 1985; Petanidou, 1991): (1) *bell*, downward-facing bell-shaped flowers where pollinators enter with all or most of their body; (2) *brush*, flower units with many protruding anthers; (3) *disk*, shallow flowers with petals spread out in a flat circle; (4) *tube*, tubular flowers which pollinators access via a proboscis or a beak; (5) *disk-tube*, a tubular stalk that ends up on a disk petal structure; (6) *funnel*, upward facing funnel-shaped flowers that pollinators enter with the entire body or much of it; (7) *flag*, the butterfly-shaped flowers of Fabaceae and Polygalaceae; (8) *gullet*, flowers with a lip serving as a landing platform for pollinators to insert their head or whole body into the corolla tube; (9) *head*, a flower aggregation functioning as a single attraction unit, i.e. densely-packed florets into inflorescences (pseudanthia); (10) *lip*, orchid flowers with an extended lip; and (11) *trap*, flowers with tubular structures that trap insects for a period of time. Examples of different floral shapes can be found in Fig. S2.1 in Appendix S2.

Floral depth – This variable describes how accessible nectar rewards are for a flower visitor. For the assessment, we categorized floral depth into three groups—short, medium and long corollas—based on their correspondence to pollinators' proboscis length. This classification followed previous studies on Mediterranean plants, such as Stefanaki et al. (2015) and Petanidou (1991), which discriminated plant taxa based on over 3000 documented plant–pollinator interactions. Thus, depending on corolla tube length, we assigned taxa to: (1) *low-depth* flowers, with <4 mm tube length; (2) *medium-depth* flowers, between 4 and 10 mm tube length; and (3) *high-depth* flowers, >10 mm tube length. The depth corresponded to keel length in flag flowers, to spathe length in trap flowers, and to the corolla tube plus spur length in spurred flowers (viz.



Country	No. of families	No. of taxa
Lebanon (LBM)	24	73
Cyprus (CYP)	40	224
Greece (GRC)	38	466
Italy (ITA)	41	646
France (FRA)	31	289
Spain (ESP)	44	925
Portugal (PRT)	39	333

Fig. 1. Map showing the Mediterranean countries in the study dataset (orange), including the number of taxa and families per country.

Violaceae, Fumariaceae, Ranunculaceae and Orchidaceae; Stefanaki et al., 2015).

Floral symmetry – Each taxon was assigned to either (1) *radial symmetry* (actinomorphic flowers) or (2) *bilateral symmetry* (zygomorphic flowers), depending on the number of symmetry axes in the flowers. Floral symmetry in Asteraceae was estimated on the basis of the whole inflorescence (Lázaro and Totland, 2014; Stefanaki et al., 2015).

Functional reproductive unit – This variable refers to inflorescences, but describes functional flower aggregations (Petanidou, 1991; Stefanaki et al., 2015) that might require different pollinator handling, influencing visitation patterns (Waser, 1983). We distinguished three levels of flower aggregations: (1) *single flowers*, which includes also any inflorescence type with ≤ five flowers open simultaneously; (2) *flat/spherical* inflorescences (such as heads, umbels, or corymbs); and (3) *cylindrical* (spikes, racemes, or panicles).

2.3.2. Other intrinsic variables

The following six additional traits were considered:

Floral colour – To include the variety of colours in the dataset, we defined six colour categories: (1) *white*; (2) *yellow, cream*; (3) *purple, pink, lilac;* (4) *red, orange, brown*; (5) *blue*; and (6) *green* (Petanidou, 1991; Petanidou and Lamborn, 2005). Whenever two or more colours appeared in an individual, the dominant one (> 50 % of flower surface) was selected; the most frequent colour was chosen for taxa in which colour differed among individuals.

Floral size – This was calculated as the average of the length and width of the exposed surface of the corolla for taxa without depth (i.e., 2D-projection; viz., disk flowers); and an average of aerial length co-considering depth and maximal width for flowers with corolla depth (i.e. 3D projection). Taxa were assigned to three levels: (1) *small*, <10 mm; (2) *medium*, 10–20 mm; and (3) *large*, >20 mm (Petanidou, 1991; Stefanaki et al., 2015). In strongly compact inflorescences (e.g. heads and compound inflorescences of Asteraceae and some Apiaceae), the whole inflorescence was considered for floral size.

Flowering season – Originally, we considered five flowering seasons: (1) *winter*, when flowering occurs mainly between December and February; (2) *spring*, when the taxa bloom mainly from March to May; (3) *summer*, when flowering occurs mainly between June and August; (4) *autumn*, when flowering occurs mainly between September and November; and (5) *all-year*, when taxa were in flower during almost the whole year. If flowering time covered two seasons, we assigned the taxa to the flowering season with the biggest overlap with the flowering peak. If flowering fell equitably in two seasons, we assigned the taxa to the earliest one. As only 12 taxa flowered all year, this category was finally removed from the analysis to avoid spurious results.

Flowering duration – The number of months a taxon is in bloom.

Life form – We assigned the study taxa to one of the following four life form categories (Petanidou et al., 1995; Stefanaki et al., 2015): (1) *therophytes*, *biennial, and monocarpic* plants; (2) *geophytes*, i.e. perennial plants with underground storage organs (bulbs, tubers, corms or rhizomes) to survive the unfavourable season; (3) *herbaceous perennials*, i.e. perennial plants either entirely herbaceous or woody only at the base; and (4) *woody perennials*, i.e. entirely woody perennial plants.

Asexual reproduction – As trustable information on the capability of plants to reproduce asexually was not found for most taxa, we decided to classify the taxa depending on whether they had structures usually associated with asexual reproduction (bulbs, tubers, corms, rhizomes, stolons, or suckers) when information on asexual reproduction was unavailable. In the case of presence, we considered them as able to reproduce asexually, otherwise we considered them unable to do so.

2.3.3. Extrinsic variables

The following five extrinsic variables were considered:

Habitat – Eight habitat types were considered (Dimopoulos et al., 2013): (1) *freshwater habitats* (aquatic habitats, springs and fens, reedbeds and damp tall-herb vegetation, seasonally flooded depressions, damp and seepage meadows, streambanks, river and lake shores); (2) *cliffs and other rocky habitats* (walls, ravines, or boulders); (3) *temperate and submediterranean grasslands* (dry and mesic pastures and meadows, rock outcrops and stony ground, or forest edges); (4) *high-mountain vegetation* (subalpine and alpine grasslands, scrub above the treeline, or screes and rocks); (5) *coastal habitats* (littoral rocks, sand dunes, salt marshes, halonitrophilous scrub or marine waters); (6) *xeric Mediterranean scrubs and grasslands* (Mediterranean scrublands, lowland screes or annual-rich pastures); (7) *agricultural and ruderal habitats* (frequently disturbed habitats, fields, plantations, roadsides, or gardens); and (8) *woodlands and scrub* (maquis and sclerophyll vegetation, broadleaved and coniferous forest, shady woodland margins, or riparian and mountain forest). If a taxon occurred in more than one habitat, we used the dominant one (or the first mentioned one if there was no information about habitat dominance).

Minimum and maximum elevation – Continuous variables denoting the minimum and maximum elevation (in m) at which each taxon has been recorded in each country.

Distribution range – A rank-measure of distribution range size, denoting the Euclidean distance between the most distant localities of each taxon (considering the overall distribution range of a species, and not the one within the country borders as considered for IUCN threat assessments). We assigned a value of 0, when taxa were extinct or extinct in the wild; a value of 1, when they had a *very limited range*, i.e., < 100 km between the most distant populations; a value of 2, when they had a *limited range*, i.e., < 250 km; a value of 3, when the taxa were *range-restricted*, i.e. < 500 km; and a value of 4, when they were *widespread*, i.e. > 500 km.

Endemicity – This variable indicated whether the taxon was endemic to a particular country.

2.4. Expert opinion about traits that define floral complexity

To gain a deeper insight in the importance of different floral traits defining complexity, we recorded the opinion of 29 world experts in pollination ecology, including the four experts that participated in Stefanaki et al. (2015). The remaining expert panel members ($n = 25$) was selected from scientists with a strong record of published empirical research on plant–pollinator interactions. Of the 70 invitations sent to participate in the survey, 25 responses were received, including those from three coauthors. The questionnaire for the experts was designed to evaluate four floral variables: floral shape, depth, symmetry, and functional reproductive unit. Each expert was asked to assign a weight (W) from 1 to 5 to each variable, based on its potential contribution to floral complexity. Additionally, the experts assigned weight to each level of the four variables (V) on a scale from 1 to 3 (except for floral shape, where the scale was set from 1 to 5 due to the high number of shapes). Lower values of W and V indicated lower complexity. The questionnaire sent to the experts was approved by the Science-Geosciences Ethics Review Board of Utrecht University (The Netherlands).

2.5. Statistical analyses

Closely related taxa may present similar traits and should not be considered independent observations (Revell, 2010). Therefore, we used Phylogenetically Informed Generalized Mixed Models (PGLMM) using the pglmm function in the phyr R package (Ives et al., 2020) in R v. 4.3.3 (R Core Team, 2024). This approach allows for phylogenetic corrections while using multiple replicates per taxon (i.e., in our dataset, the same taxon could appear in different countries with different vulnerability statuses). Thus, to evaluate how different intrinsic and extrinsic variables influence plant vulnerability, we ran a PGLMM including both types of variables with a binomial error distribution (response: more vs. less threatened) in which the predictors were the intrinsic and extrinsic variables described in the section “Variables potentially related to plant vulnerability”. As there might be strong correlations between several study plant traits, we first evaluated correlations and associations between predictor variables (Table S2.2 in Appendix S2). Based on this, we excluded flower symmetry, which was highly associated to flower shape, minimum elevation, which was highly correlated with maximum elevation, and asexual reproduction and endemicity, which were related to life form and distribution range, respectively (Table S2.2). On the model with the remaining fixed variables, we then ran VIF analyses using the check_collinearity function in the performance R package (Lüdecke et al., 2021), and additionally excluded life form from the predictors to leave a set of variables without multi-collinearity

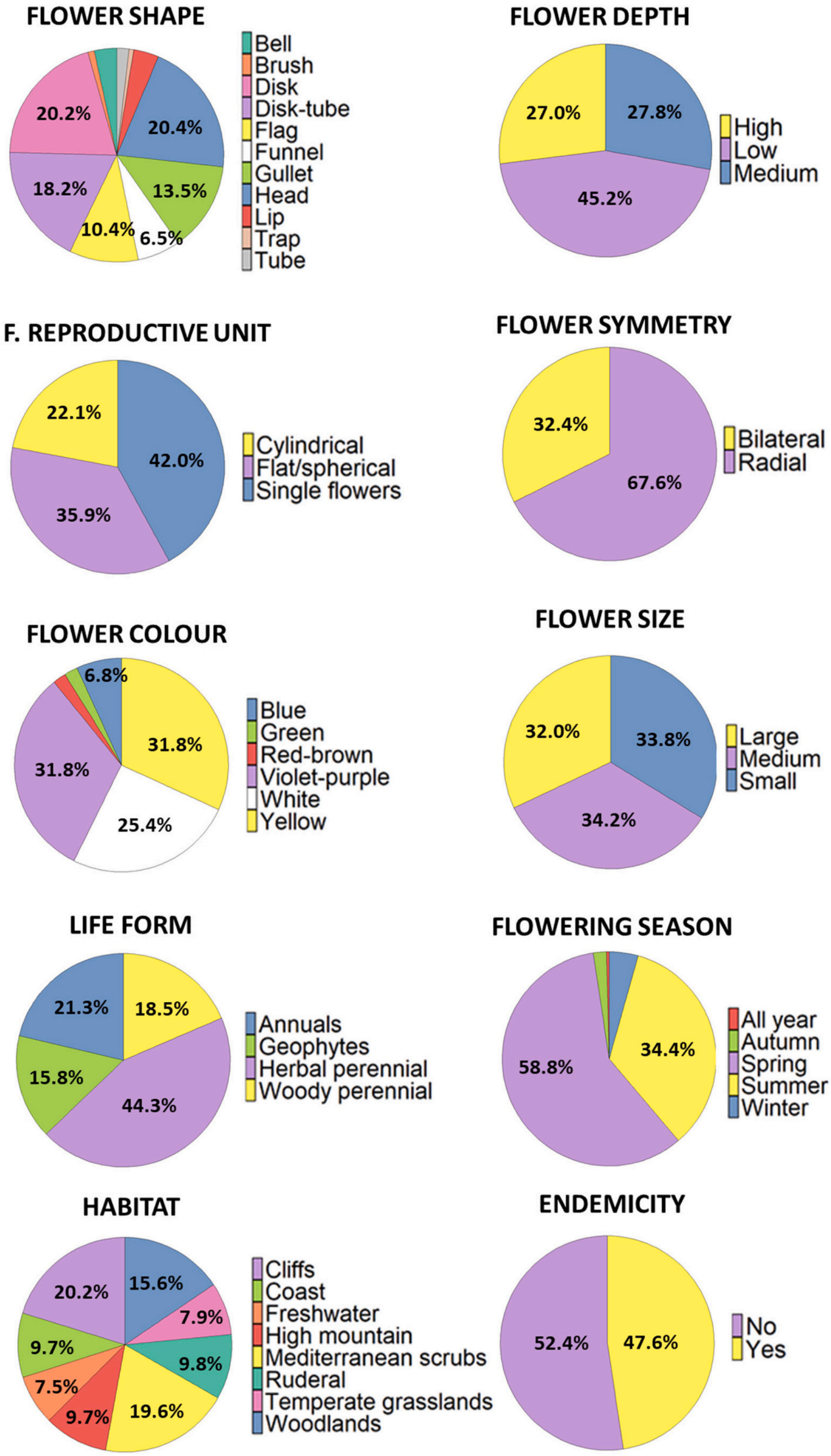


Fig. 2. Pie charts showing the distribution of categorical variables among the taxa included in the dataset. Percentages are displayed for all the categories with >5 % of the taxa.

problems. In the PGLMM, both countries and taxa were included as crossed random factors. To inform the PGLMM phylogenetically, we previously built the phylogenetic relationships among the study plant taxa using the phylo.marker function in the V.phylomaker R package (Jin and Qian, 2019). This function matches a given species list to the mega tree "GBOTB.extended.tre" which resulted from the merge of two previous mega trees (Zanne et al., 2014; Smith and Brown, 2018) and includes 74,533 species and branch lengths corresponding to chronological times (millions of years). Plant taxa that did not appear in the mega tree were inserted into randomly selected nodes below the genus or family level basal nodes (Scenario 2; Qian and Jin, 2016; Jin and Qian, 2019). Preliminary analyses of the phylogenetic signal in the vulnerability status of plant taxa conducted separately for each country (D statistic for binary traits using the phylo.D function in the caper R package; Fritz and Purvis, 2010; Orme et al., 2023) revealed that there was significant phylogenetic signal in 4 of the 7 study countries (Table S2.3 in Appendix S2), supporting the use of phylogenetically informed analyses. The significance of fixed and random variables was calculated using Likelihood Ratio Tests (LRT), and the significance of the levels within significant factors is based on contrasts. Predictive R^2 was calculated using the R2 function in the rr2 R package (Ives, 2018; Ives and Li, 2018). Plots were drawn using the ggplot2 R package (Wickham, 2016).

To analyze the results of experts' opinions on traits more related to floral complexity, we used five Generalized Linear Mixed Models (GLMMs), one model to compare the weight given to the four main floral traits, and one for each of the traits separately, using the glmer function in the lme4 R package (Bates et al., 2015) in R version 4.3.3 (R Core Team, 2024). In all these models, the trait was the predictor variable, the weight given by experts the response variable, and the expert identity the random factor. Due to the nature of the data, we used Poisson error distributions with log link functions. The significance of fixed factors was calculated using Likelihood Ratio Tests (LRT), and post hoc analyses were run using the emmeans function in the emmeans R package (Lenth, 2024). Plots were drawn using the ggplot2 R-package (Wickham, 2016).

3. Results

Fig. 2 shows the distribution of categorical variables among the study taxa. The most common floral shapes were heads, disk and disk-tube flowers, with ca. 20 % of the taxa each. Most flowers also had low depths (ca. 45 %), single flowers (ca. 42 %), and radial symmetry (ca. 68 %), although the rest of the categories had good representation with >20 % of the taxa. The most prominent colours were yellow, violet-purple and white, with 25–32 % of the taxa each. All floral sizes were equally represented (32–34 % of the taxa in each category). Most taxa flowered in spring (ca. 59 %) and summer (ca. 35 %) and correspond to perennial herbs (ca. 44 %). Regarding extrinsic variables, all eight habitats were well distributed among the study taxa, as each of them represented between 7 % and 20 %. More than half of the taxa were non-endemic to the study countries. The minimum elevation varied between 0 and 3000 m (mean ± SE: 490.62 ± 11.34), whereas the maximum elevation varied between 0 and 3600 m (1026.87 ± 14.29). There were representatives of all distribution ranges (*extinct or extinct in the wild*: 6 species; *very limited range*: 1104; *limited range*: 367; (3) *range-restricted*: 250; *widespread*: 1229).

3.1. Intrinsic variables driving vulnerability in the Mediterranean flora

Three of the evaluated plant traits had significant effects on plant vulnerability (more vs. less threatened): floral shape, functional reproductive unit and flowering duration (Table 1A). Regarding floral shape, plants with lip and flag flowers were found to be significantly more threatened than plants with disk-tube, funnel, tube and bell flowers, which showed the lowest plant vulnerability (Table 1A; Fig. 3A). Although brush flowers also showed high vulnerability (Fig. 3A), post hoc analysis indicated no significant differences from other shape categories. The other flower shapes (disk, head gullet and trap) showed intermediate vulnerability levels (Fig. 3A). Plant vulnerability was lowest in taxa with flat-spherical inflorescences compared to taxa with cylindrical inflorescences or solitary flowers (Table 1A; Fig. 3B). The proportion of more threatened taxa also decreased with a longer flowering duration (Fig. 3C).

Table 1

Results of the PGLMMs showing the effect of several intrinsic and extrinsic variables on the vulnerability (more vs. less threatened) of Mediterranean plant species included in Red Data Books. Significant results are based on Likelihood Ratio Tests. *P*-values are marked in bold when significant ($p \le 0.05$). Predictive R^2 for fixed effects is 0.14.

Fixed effects	χ^2	*df*	*p*
A. Intrinsic variables			
Flower shape	20.85	10	**0.022**
Flower depth	0.52	1	0.471
Functional reproductive unit	11.01	2	**0.004**
Flower colour	6.74	5	0.241
Flower size	2.41	2	0.300
Flowering season	5.19	3	0.158
Flowering duration	3.88	1	**0.049**
B. Extrinsic variables			
Habitat	43.33	7	**< 0.0001**
Maximum altitude	54.71	1	**< 0.0001**
Distribution range	24.48	1	**< 0.0001**

Random effects	Variance	Std.Dev	Significance
Phylogenetic signal	0.003864	0.06216	$\chi^2 = 2.98$; $df = 1$, $p =$ **0.007**
Species	0.002604	0.05103	$\chi^2 = -0.0003$, $df = 1$, $p = 1$
Country	1.052910	1.02611	$\chi^2 = 75.74$, $df = 1$, $p <$ **0.0001**

3.2. Extrinsic variables driving vulnerability in the Mediterranean flora

All evaluated extrinsic variables significantly impacted plant vulnerability (Table 1B). There was a significantly higher percentage of more threatened taxa in coastal and freshwater habitats, whereas high mountains, scrubs, and cliffs were the habitats with a lower percentage of more threatened taxa (Table 1B; Fig. 4A). The proportion of more threatened taxa also decreased with maximum elevation (Fig. 4B) and distribution range (Fig. 4C).

3.3. Experts' opinions on traits related to floral complexity

In line with the results of this study, pollination experts considered floral shape to be the variable most closely related to floral complexity, although differences among floral traits were marginally non-significant ($\chi^2 = 7.26$; $df = 3$; $p = 0.064$; Fig. 5A). The experts agreed, though, that different floral shapes represented different floral complexities. For them, flowers with flag, gullet, trap, lip, and tube shapes showed the highest complexity, and disk, brush and head shapes were those with the lowest complexity, whereas the other shapes (bell, funnel, disk-tube) presented intermediate complexity ($\chi^2 = 89.80$; $df = 10$; $p < 0.0001$; Fig. 5B). Overall, the experts also agreed that floral complexity increased with the depth of the corolla tube ($\chi^2 = 24.11$; $df = 2$; $p < 0.0001$; Fig. 5C), and was highest in bilateral flowers ($\chi^2 = 13.26$; $df = 1$; $p = 0.0003$; Fig. 5D), and cylindrical inflorescences ($\chi^2 = 6.66$; $df = 2$; $p = 0.036$; Fig. 5E).

4. Discussion

We showed that several floral and plant traits, as well as extrinsic variables, were related to the vulnerability of Mediterranean plants. There were proportionally more threatened species among those with

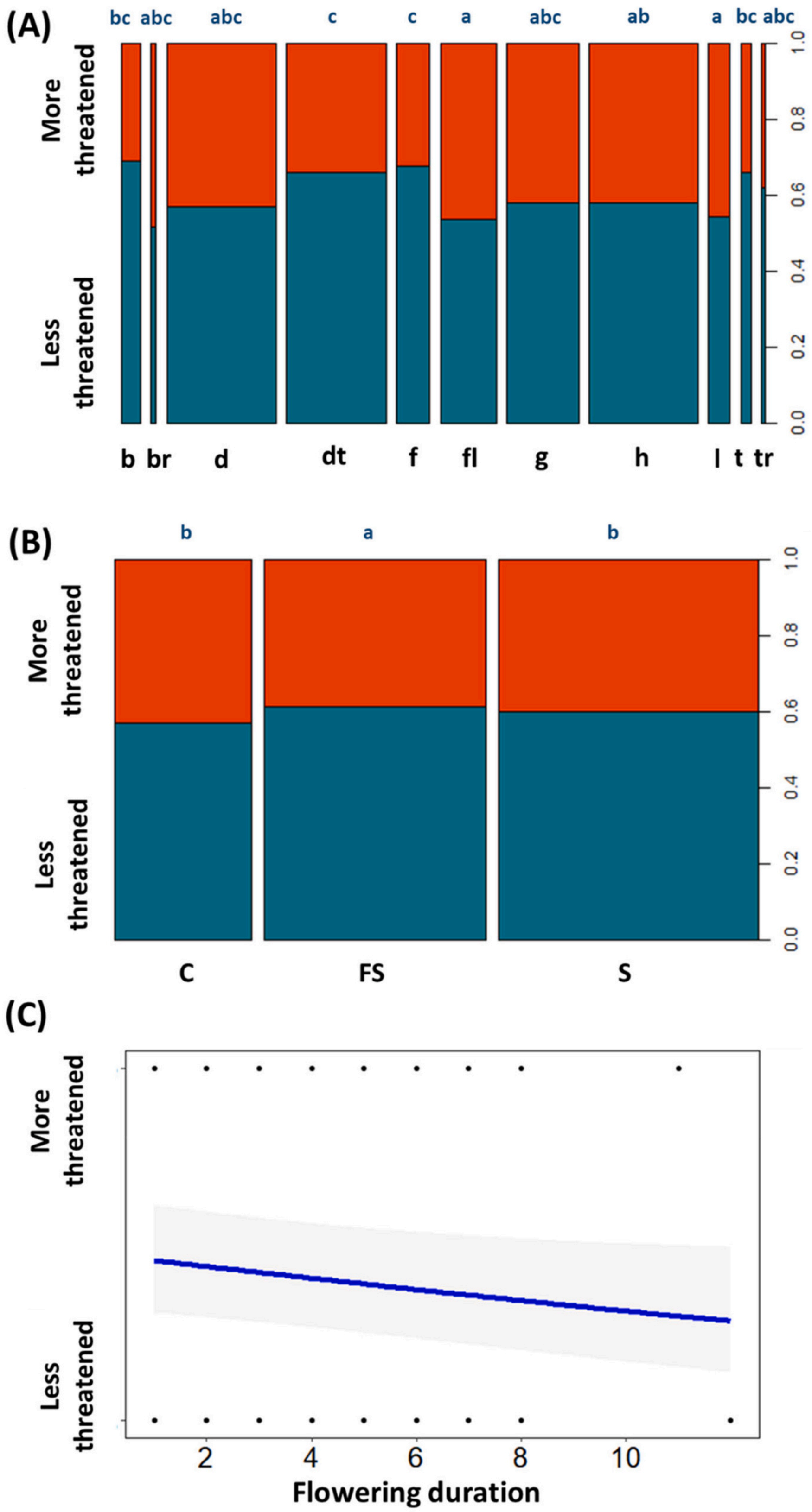


Fig. 3. Effect of floral traits and flowering duration on the vulnerability of Mediterranean plant taxa. (A) Spine plot showing the percentage of taxa more and less threatened per floral shape. b: bell; br: brush; d: disk; dt: disk-tube; f: funnel; fl: flag; g: gullet; h: head; l: lip; t: tube; and tr: trap. (B) Spine plot showing the percentage of taxa more and less threatened per functional reproductive unit (S: solitary flowers; C: cylindrical inflorescences; FS: flat-spherical inflorescences). The width of the bars represents the number of taxa within each category. Different letters above the bars indicate significant differences among levels of the variables. (C) Relationship between flowering duration and the taxa threatened status.

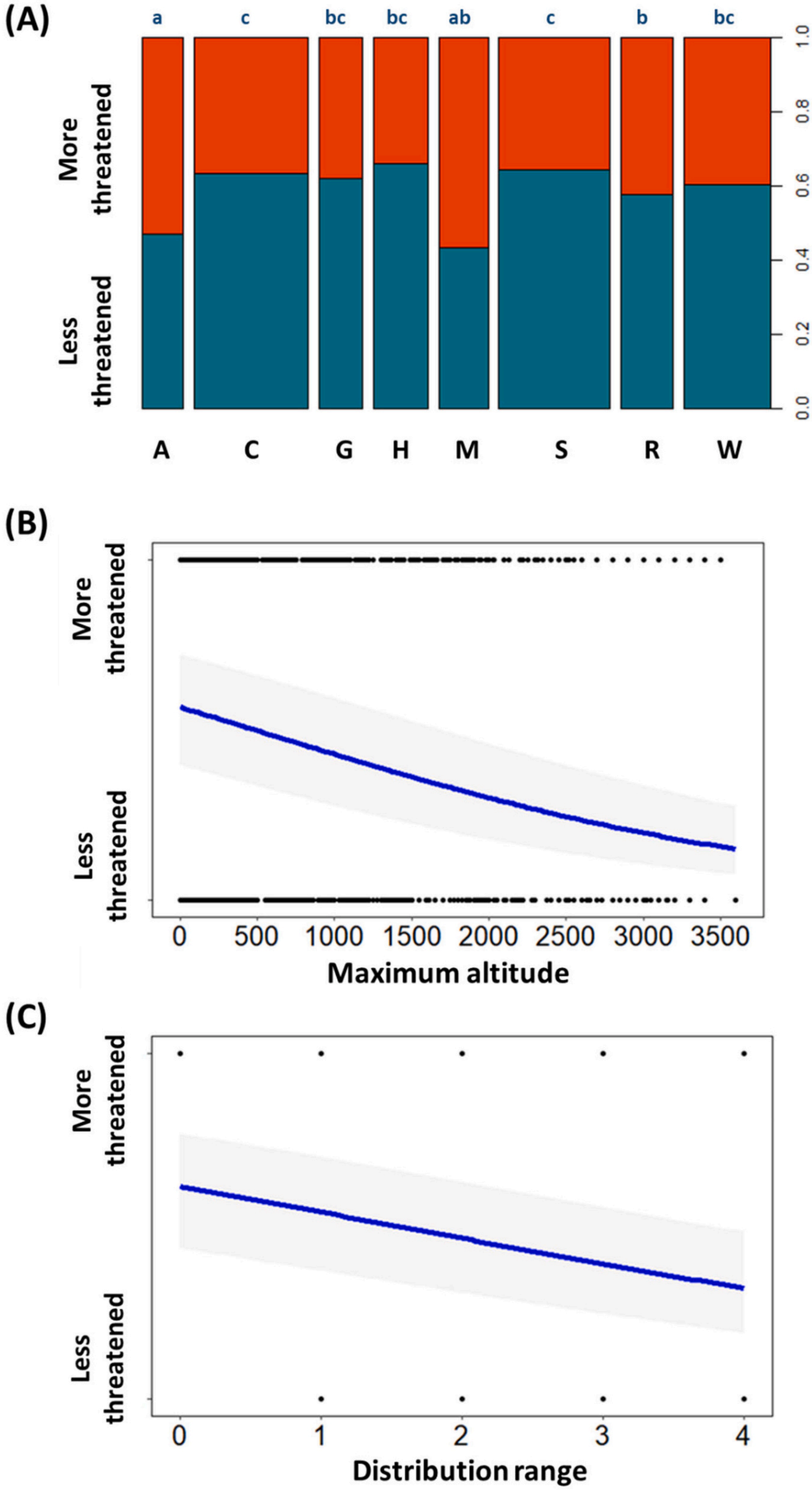


Fig. 4. Effect of extrinsic variables on the vulnerability of Mediterranean plant taxa. (A) Spine plot showing the percentage of taxa more and less threatened per habitat (A: Freshwater habitats; C: Cliffs and other rocky habitats; G: Temperate and submediterranean grasslands; H: High-mountain vegetation; M: Coastal habitats; S: Xeric Mediterranean scrubs and grasslands; R: Agricultural and ruderal habitats; W: Woodlands and scrubs). The width of the bars represents the number of taxa within each category. Different letters above the bars indicate significant differences among levels of the variables. (B) Relationship between maximum elevation and the threatened status of Mediterranean taxa. (C) Relationship between the distribution range of taxa and their threatened status.

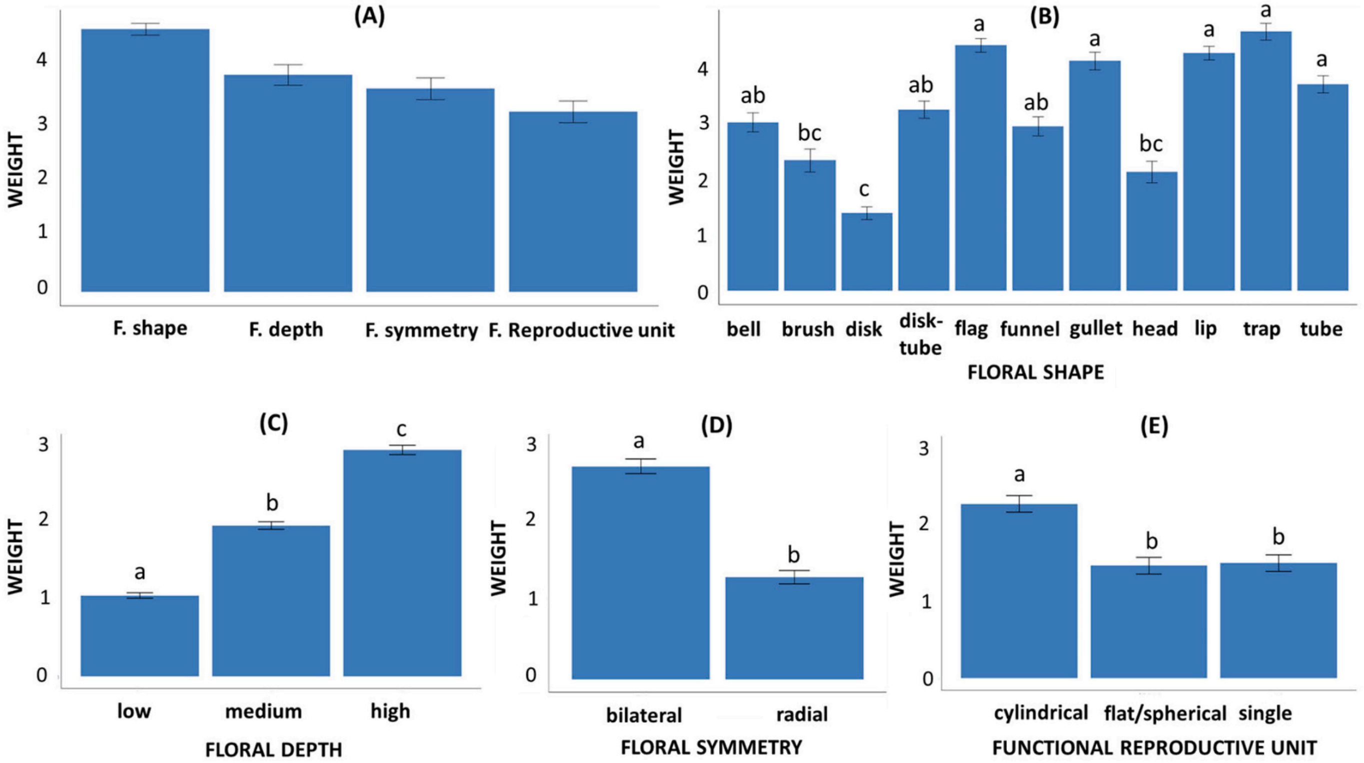


Fig. 5. Expert opinions regarding the floral traits more related to floral complexity: (A) average (± SE) weight given to each of the four floral traits related to floral complexity; (B) average (± SE) values given to each floral shape; (B) average (± SE) values given to each level of floral depth; (C) average (± SE) values given to each category of floral symmetry; and (D) average (± SE) values given to each category of functional reproductive unit. Different letters above the bars indicate significant differences among levels of the variables.

more complex floral shapes. Vulnerability was also higher in plant taxa with cylindrical inflorescences or solitary flowers compared to flat-spherical inflorescences, and decreased with flowering duration. Regarding extrinsic variables, we found that coastal and freshwater habitats had a significantly higher percentage of more threatened taxa. In addition, plant vulnerability increased as the distribution range and the maximum elevation of taxa decreased.

4.1. Intrinsic variables driving plant vulnerability in the Mediterranean flora

Floral shape, functional reproductive unit, and flowering duration influenced plant vulnerability. We expected plants with complex and specialised floral morphologies to be more vulnerable than those with simpler floral morphologies because the former depend on specialised pollinators or behaviours to be effectively pollinated, whereas less complex flowers may have a more generalized pollination system (Fenster et al., 2004; Lázaro et al., 2008; Watts et al., 2016; Yoder et al., 2020; Bergamo et al., 2021). According to our expectations, floral shape was the floral variable that influenced plant vulnerability the most. Floral shape can be viewed as a combination of various traits such as symmetry and depth, which we also considered in this study. Therefore, it is not surprising that floral shape alone is the variable that mostly influences overall plant vulnerability patterns. We found that plants with lip, flag and brush flowers were those most threatened, although post hoc analysis revealed that brush flowers did not differ from other floral shapes, likely due to the low number of taxa within this category. The most threatened floral shapes (viz. lip and flag) were among those identified as more complex by world experts, which is also in line with our initial expectation that floral complexity is related to higher vulnerability in plants because specialized taxa tend to be the most vulnerable (Clavel et al., 2011). It is notable that although brush flowers were considered by experts as having simple morphologies, they have been shown to be specialized (Olesen et al., 2007) and vulnerable regarding their floral shapes (this study). Likely, the long, dense and stiff stamens and styles of brush flowers make nectar harvesting difficult for many pollinators (Olesen et al., 2007). Interestingly, disk, head, gullet, and trap flowers showed intermediate vulnerability, so the least threatened taxa were not those bearing flowers with the simplest morphologies (such as disk flowers). Instead, the least threatened taxa were those bearing flowers with intermediate morphological complexities (such as bell, funnel, disk-tubular, and tubular flowers). This can be potentially explained by the generalization level of plant species with such floral morphologies. Using data on 37 plant–pollinator networks, Olesen et al. (2007) showed that species' generalization level (i.e., diversity of pollinators) was highest in tube (including disk-tube), bell/funnel, and dish/bowl flowers, while it was lower in flag, head/brush, and gullet flowers (they did not analyze lip flowers). Similar results were also found by Ramírez (2003), who showed that bell, tube, and dish flowers were more generalist than trap, gullet and flag flowers when pollinator species were sorted into pollinating agent classes. Tube, bell and funnel flowers might have high generalization levels because the number of pollinators that a plant species receives not only depends on how accessible their nectar and pollen rewards are, but also the morphology and behaviour of pollinators and the diversity of species within pollinator functional groups (Olesen et al., 2007). Overall, it seems likely that a higher pollinator generalization in flowers with intermediate complexities may explain why these taxa are associated with lower vulnerability in our Mediterranean dataset. Alternatively, it cannot be discarded that flowers with full open access to all insect visitors (e.g. disk flowers) could suffer from higher pollen removal by pollen thieves and unfaithful pollinators than other more specialized shapes (Gross and Mackay, 1998; Hargreaves et al., 2009); intermediate floral complexities (bell, funnel, disk-tube flowers) may allow access to many pollinators while protecting floral rewards. Another reason could be that under the warm and dry Mediterranean conditions, disk flowers may be rather vulnerable due to heat, being frequently non-nectariferous (e.g. *Fumana, Papaver, Tulipa*) and/or with a short flower life span, normally of one day (e.g. *Cistus* species), thus less alluring or available to pollinators (Petanidou, 1991; Petanidou et al., 1995).

We also expected a differential effect of floral aggregations (functional reproductive units) on plant vulnerability, since changes in inflorescence size, density and shape may influence inflorescence handling by pollinators and, therefore, pollinator visitation patterns (Linhart, 1973; Ohara and Higashi, 1994). As expected, we found that flat-spherical inflorescences were less threatened than cylindrical inflorescences and single flowers. This might be because flat-spherical inflorescences function as large attractive units that might be handled as a single entity providing ample space to insect visitors to land and walk while exploring the florets; in other words, flat-spherical inflorescences may constitute a surface continuum not requiring particular handling capacity. The lower vulnerability of these flat-spherical structures might also be related to the higher attractiveness of large flower units (Bell, 1985; Eckhart, 1991; Lázaro et al., 2008, 2020), as flat-spherical inflorescences are often much larger than single flowers in Mediterranean systems. On the other hand, cylindrical inflorescences are more difficult to handle than single flowers and flat-spherical inflorescences, as they are typically related to specific behaviours of pollinators that normally approach the inflorescences from the bottom, scrabble upwards and quit the spike before visiting all the flowers (Waser, 1983). Moreover, in cylindrical inflorescences of non-rewarding species (e.g., many orchids) pollinators fly away after having visited the first flower (Jersáková et al., 2006; Capó et al., 2023), which may affect the reproduction of species with this type of inflorescences. Interestingly, cylindrical inflorescences were also assigned by world experts as the most complex inflorescence type.

Lastly, we found that plant vulnerability decreased with flowering duration. This is not a surprise since the longer the flowers are available for pollinators, the higher the probability that they are visited by more pollinator individuals and species due to temporal turnover (Høye et al., 2013; Lázaro et al., 2020). In line with our results, previous studies in Finland (Lahti et al., 1991) and the Czech Republic (Gabrielová et al., 2013) showed that more threatened species flowered for shorter periods, beginning to flower later and concluding earlier than less threatened species. Although this pattern could sometimes arise due to the small population sizes (i.e. the larger the plant population the more staggered the flowering) and restricted geographical distributions of the most endangered taxa (Lahti et al., 1991), this might not be the case here, because we used very wide characterizations of flowering periods (number of months in flower), and because flowering duration and distribution range were not correlated in our study system (Table S2.2).

We expected plant vulnerability to be affected by other floral and plant traits, such as floral colour and size, plant flowering season and life form, since these variables are known to influence pollination patterns and plant reproductive strategies (Lovett Doust and Lovett Doust, 1988; Lázaro et al., 2008; Rafferty and Ives, 2010; Petanidou et al., 2014; Bergamo et al., 2021). However, none of these variables appeared to have a significant effect on the vulnerability of the studied threatened Mediterranean flora. The lack of effect of flowering season is perhaps due to different responses depending on the bioclime, with plants tending to flower earlier in drier areas and postpone flowering in cooler ones (Willems et al., 2022). Contrary to our results, Stefanaki et al. (2015) found a significant effect of life form on plant vulnerability for the Greek flora, with woody perennials being the least vulnerable, perhaps because of the drier and hotter eastern Mediterranean conditions. However, the lack of effect of life form on overall vulnerability patterns may be also related to the fact that plants respond to different anthropogenic pressures depending on their life form, not being a single trend. For instance, Fois et al. (2018) showed local extinctions of therophytes were strongly related to fires while extinctions of woody perennials were more related to urbanization and road construction.

As an epitome, the finding that floral shape, reproductive unit and flowering duration are associated with plant vulnerability suggests that pollination failure may be more pronounced in taxa with more specialized floral shapes and shorter phenologies and, thus, the above traits may constitute a major underlying reason for the vulnerability of Mediterranean plants. Indeed, it is highly remarkable that floral traits significantly affect plant vulnerability even though IUCN assessments are almost exclusively based on extrinsic factors, and especially considering that our analysis was only based on threatened taxa (more vs. less threatened, excluding least concerned taxa – LC); which suggests that a comparison between the entire set of threatened vs. non threatened taxa would have shown even stronger effects. Our analysis indicates overall patterns across most entomophilous plant families in the studied Mediterranean countries, using data on plant taxa currently listed in Red Data Books. We expect, however, that if the whole flora of each study country had been assessed under IUCN criteria, additional interesting patterns would have arisen. Such patterns may be even clearer if studies focus on particular ecological regions or systems. For example, considering that a great part of the study area belongs to islands, we expect that analysing separately island vs. mainland zones, i.e. by unmasking the effect of colonization-filter hypothesis (known as Baker's law), may reveal even more interesting results (see e.g. Grossenbacher et al., 2017). Similarly, the importance of different plant traits for vulnerability might differ among plant families, and there might be plant traits not considered here, such as different rewards offered to pollinators, flower colours as seen by insects, fecundity, or the existence of different pollination modes and mating systems (e.g., selfing vs. outcrossing plants), that could additionally affect the vulnerability of particular plant taxonomic groups (Culley et al., 2002; Shivanna, 2015; Charitonidou and Halley, 2020). In any case, the large-scale overall patterns found here suggest that floral shape, reproductive unit, and flowering duration might be carefully considered to develop preventive conservation measures and establish priorities for conservation assessment for unevaluated Mediterranean taxa when field data are limited or unavailable.

4.2. *Extrinsic variables driving vulnerability in the Mediterranean flora*

All the extrinsic variables studied here (habitat, maximum elevation, and distribution range) were found to have a significant impact on the vulnerability of Mediterranean plants. Coastal and freshwater areas were the habitats with a significantly higher proportion of more threatened taxa. In contrast, woodland along with scrubs and cliffs were the habitats with a higher proportion of less threatened taxa. The higher vulnerability in coastal and freshwater habitats might be related to severe human pressures, as these habitats across the Mediterranean Basin are exposed to high levels of anthropogenic disturbance (Médail, 2017, and references therein) due to habitat destruction and climate change, and in particular, wetland draining and urbanization related to tourism. Similar results have been reported for coastal zones of other Mediterranean areas, such as Sardinia (Bacchetta et al., 2012) and Greece (Stefanaki et al., 2015). Besides, although there is a significant knowledge gap regarding the distribution and conservation of plant species in Mediterranean wetlands, at least 339 taxa endemic to Europe are known to occur regularly in wet habitats (Hobohm and Bruchmann, 2011), and approximately 25 % of species of lentic wetlands have been identified as endangered or with unknown conservation status in the Mediterranean islands of Sardinia, Corsica, Sicily and Malta (Fois et al., 2024). Indeed, it is well-known that freshwater ecosystems are heavily impacted by human activity, such as flow modification, water pollution, destruction or degradation, and invasive species (e.g. Dudgeon et al., 2006; Gozlan et al., 2019). Besides, plant vulnerability decreased with maximum elevation, indicating that taxa living in areas more inaccessible to humans are less threatened. A previous study on a smaller geographical scale (Greece: Stefanaki et al., 2015) did not find a clear relationship between elevation and plant vulnerability, but this pattern clearly emerged in our study that considered larger geographical and elevational scales. However, the importance of monitoring high-mountain species in conservation programmes should not be overlooked, since these species are vulnerable in the context of climate change (Engler et al., 2011; Pauli et al., 2012), the composition of their pollinator assemblages may drastically change to cope with climate (Minachilis et al., 2021), and some species may suffer other pressures beyond those directly related to their pollination success (see e.g. Cuena-Lombraña et al., 2018a, 2018b).

Lastly, indicators of distribution ranges are fundamental in estimating a species' conservation status sensu IUCN. Therefore, it is not surprising that we found significant effects of this variable on plant vulnerability. As expected, we found a negative relationship between plant vulnerability and the distribution range of species, highlighting that taxa with more restricted ranges were more threatened than those spreading over larger areas. Overall, our results highlight the importance of focusing conservation efforts on range-restricted taxa, lowlands, and coastal and wetland habitats experiencing high human pressure.

5. Conclusions

Our work stresses the need to incorporate floral traits and other intrinsic and extrinsic variables not currently considered in IUCN criteria to improve plant conservation strategies. We show that floral shapes such as lip and flag—considered among the most complex by pollination experts—along with cylindrical inflorescences, solitary flowers, and shorter flowering durations, are associated with increased plant vulnerability. In addition, plant taxa living in lowlands, coastal and freshwater areas, and having smaller distribution ranges are the most threatened in the Mediterranean countries examined here. The above traits could be used as a basis for managers and practitioners in the area to develop preventive conservation measures and to prioritise conservation assessments where field data are limited, inadequate or unavailable. To this end, we recommend future research in larger areas or other ecogeographical regions in Europe, which may reveal additional patterns, deepening our understanding on the effects of floral complexity on plant vulnerability.

CRediT authorship contribution statement

Amparo Lázaro: Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Anastasia Stefanaki:** Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Martha Charitonidou:** Data curation, Visualization, Writing – review & editing. **Joana Cursach:** Investigation, Data curation, Writing – review & editing. **Maria Panitsa:** Data curation, Writing – review & editing. **Ioannis Bazos:** Data curation, Writing – review & editing. **Rosa Ranalli:** Investigation, Writing – review & editing. **Mauro Fois:** Investigation, Writing – review & editing. **Marta Galloni:** Investigation, Writing – review & editing. **Gianluigi Bacchetta:** Investigation, Writing – review & editing. **Sílvia Castro:** Investigation, Writing – review & editing. **João Loureiro:** Investigation, Writing – review & editing. **Katerina Goula:** Investigation, Writing – review & editing. **Luis Navarro:** Investigation, Writing – review & editing. **Magda Bou Dagher Kharrat:** Investigation, Writing – review & editing. **Rhea Kahale:** Investigation, Writing – review & editing. **Nathalie Machon:** Investigation, Writing – review & editing. **Gabrielle Martin:** Investigation, Writing – review & editing. **Udayangani Liu:** Investigation, Writing – review & editing. **Giovanna Aronne:** Investigation, Writing – review & editing. **Živa Fišer:** Investigation, Writing – review & editing. **Theodora Petanidou:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare no known competing financial or personal interests that could have influenced the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111626.

Data availability

Data will be made available on request.

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