Plant Ecology and Evolution 159 (3): 588–598, 2026
https://doi.org/10.5091/plecevo.201010

RESEARCH ARTICLE

Climatic niche conservatism and Pleistocene range dynamics in two Mediterranean *Cistus* species

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Academic editor: Lorenzo Lazzaro ♦ **Received** 24 May 2026 ♦ **Accepted** 1 September 2026 ♦ **Published** 25 September 2026

Abstract

Background and aims – Understanding how closely related species diverge is a fundamental issue in evolutionary biogeography, particularly in regions formed by repeated climatic oscillations. We examined the drivers of geographic separation between *Cistus albidus* and *Cistus creticus* across the Mediterranean Basin. We tested whether their divergence reflects climatic niche differentiation or historical geographic isolation associated with potential refugial patterns.
Material and methods – We combined ensemble species distribution modelling, palaeoclimatic projections, climatic niche analyses in environmental space, and plastid *trnL–trnF* sequence-based haplotype analysis. Models were calibrated under current climatic conditions and projected to past periods to identify suitable areas and potential refugial patterns. Niche overlap and dynamics were assessed using Schoener's D, Warren's I, stability, expansion, and unfilling.
Key results – The species showed moderate climatic niche overlap, high niche stability, and little evidence of strong climatic niche divergence. Palaeoclimatic models revealed geographically structured suitable areas, while genetic analyses indicated partial differentiation together with widespread sharing of the dominant haplotype. Overall, the results support a stronger role for geographic history and Pleistocene range dynamics than for climatic niche separation.
Conclusion – The divergence between *Cistus albidus* and *Cistus creticus* appears to have been shaped primarily by historical geographic isolation and potential refugial patterns rather than by major shifts in climatic niches. This study highlights that Mediterranean plant divergence may proceed under climatic niche conservatism, with historical range changes playing a central role in structuring regional biodiversity.

Keywords

biogeography, climatic niche conservatism, genetic structure, Mediterranean Basin, Pleistocene, Quaternary refugia, species distribution models

INTRODUCTION

Understanding the processes that drive species divergence is a main goal in evolutionary biology. Speciation patterns can be shaped by multiple mechanisms, such as geographic and ecological isolation, genetic processes, and non-adaptive mechanisms occurring at different levels (Turelli et al. 2001; Rieseberg and Willis 2007; Fitzpatrick et al. 2009). At the ecological level, species may diverge either by adapting to different climates or by maintaining their ancestral climate preferences (Wiens et al. 2010). Climatic niche divergence occurs when populations adapt to different environments and may lead to reproductive isolation (Wiens 2016). Conversely, niche conservatism suggests that species maintain ancestral climatic preferences, so divergence occurs primarily through geographic isolation rather than ecological variation (Wiens 2004; Rundle and Nosil 2005; Schluter 2009).

The Mediterranean Basin provides a particularly suitable system for examining these processes. The region has experienced complex geological and climatic changes, including tectonic fragmentation, the Messinian salinity crisis, and repeated Pleistocene climatic oscillations (Thompson et al. 2026). These events have shaped a diverse, mosaic-like landscape in which multiple

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refugial areas and distinct regional patterns are evident across many plant lineages (Médail and Diadema 2009; Thompson 2020). Clear east–west differentiation is seen in several Mediterranean tree lineages. *Pinus halepensis* Mill. is widespread in the western Mediterranean, whereas its relative *P. brutia* Ten. occurs mainly in the east (Barbéro et al. 1998). A similar pattern is found in junipers, with *Juniperus thurifera* L. confined to mountainous areas of the western Mediterranean and its eastern vicariant, *J. excelsa* M.Bieb., occurring across the mountains of the eastern part of the Basin (Barbero et al. 1994). The Mediterranean Basin has been formed by a complex geological history, repeated climatic changes, and strong ecological variation. These conditions allowed ancient lineages to persist in stable refugia while also creating opportunities for more recent diversification, which may help explain the region's high endemism and exceptional biodiversity (Médail and Quézel 1997).

The genus *Cistus* L. (Cistaceae) represents a suitable system for exploring these questions. Within this genus, *Cistus albidus* L. and *Cistus creticus* L. are closely related, purple-flowered taxa that exhibit a largely allopatric distribution across the Mediterranean Basin (Guzmán and Vargas 2005; Guzmán et al. 2009; Lukas et al. 2021). *Cistus albidus* is primarily restricted to the western Mediterranean, whereas *C. creticus* occurs mainly in central and eastern regions. Their distributions overlap only in Morocco, southern Spain and France, and northern Italy, as well as on the islands of Sardinia and Corsica. Despite their clear west–east separation, both species can grow on calcareous or basic substrates, unlike many other purple-flowered *Cistus* species (Civeyrel et al. 2011). This combination of ecological similarity and geographic separation makes them a useful system for examining whether their divergence was shaped mainly by climatic niche differences or by historical geographic isolation.

Molecular clock calculations date the last common ancestor of *C. albidus* and *C. creticus* to approximately 0.19 Myr ago, with an estimated range of 0.33–0.01 Myr (Guzmán et al. 2009). This estimate suggests that their divergence occurred during the late Pleistocene. Previous studies have examined the genetic diversity and evolutionary relationships between *C. creticus* and *C. albidus* (Guzmán and Vargas 2005; Lukas et al. 2021). However, these studies have primarily focused on intraspecific variation and phylogenetic relationships and have not directly examined how climatic niche dynamics and historical refugial processes have determined present-day distributions.

This study investigates whether the west–east separation between *C. albidus* and *C. creticus* is better explained by historical geographic isolation or by climatic niche divergence. If historical isolation and potential refugial dynamics play the main role, we expect the two species to retain broadly similar climatic niches while their suitable areas maintain a persistent west–east spatial separation over time. Some genetic differentiation between the species may also be expected as a consequence of reduced gene flow. In contrast, if climatic niche divergence has played a stronger role, we expect lower niche overlap and clearer separation in climatic space. We test these alternatives using species distribution modelling, palaeoclimatic projections, climatic niche analyses, and plastid haplotype data.

MATERIAL AND METHODS

Species distribution modelling and palaeoclimatic projections

We reconstructed the past potential distributions of *Cistus creticus* and *Cistus albidus* using species distribution modelling (SDM). We obtained species occurrence records from GBIF (Global Biodiversity Information Facility 2025a, 2025b). We removed records with missing or duplicate coordinates, reported coordinate uncertainty greater than 10 km, implausible geographic positions identified using the R package CoordinateCleaner v.3.0.1 (Zizka et al. 2019), and a non-wild occurrence status. We retained records without coordinate-uncertainty information. We included records classified by GBIF as HumanObservation, Observation, or PreservedSpecimen. We developed country-level native-range masks based on WGSRPD Level 3 regions reported in Plants of the World Online (POWO 2026) and further validated the distributions regionally for France and Italy. We evaluated French records using Tela Botanica (Julve 2018), and Italian records using the regional status reported by the Portale della Flora d'Italia (Società Botanica Italiana 2026), excluding records classified as erroneous or naturalised. We reduced spatial clustering by thinning occurrence records to a minimum distance of 5 km with the R package spThin v.0.2.0 (Aiello-Lammens et al. 2015). We ran 100 repetitions and retained the replicate containing the largest number of records. The final dataset included 6,420 spatially filtered records, with 4,144 records for *Cistus albidus* and 2,276 for *Cistus creticus*. One *C. albidus* record was excluded during model fitting because it fell in a raster cell with missing predictor values. The final model-calibration dataset therefore included 6,419 occurrence records. We obtained current and palaeoclimatic bioclimatic variables from the PaleoClim database, using climatic layers at a spatial resolution of 2.5 arc-minutes (Brown et al. 2018). Current climatic conditions represented the period 1979–2013 and were based on CHELSA-derived climate data (Karger et al. 2017). We also checked the quarter-based bioclimatic variables for abrupt spatial changes before selecting the final predictor set. BIO8 and BIO9 showed much stronger local temperature discontinuities than the other temperature variables, so we excluded them from further analysis. To reduce multicollinearity among predictors, we first removed strongly correlated predictors using a Pearson correlation threshold of $|r| =$

0.70. We then applied variance inflation factor analysis in the R package usdm v.2.1-7, retaining variables with VIF values below 10 (Naimi and Araújo 2016). The final predictor set included five bioclimatic variables: BIO1, BIO3, BIO4, BIO14, and BIO19.

To estimate species distribution models under current climatic conditions, we used an ensemble modelling approach that combined Random Forest (RF), Generalised Linear Models (GLM), Maximum Entropy modelling (MaxEnt), and Boosted Regression Trees (BRT), as implemented in the R package sdm v.1.2-55 (Naimi and Araújo 2016). The two species were modelled separately, using presence records together with 10,000 randomly selected background points for each species. To test whether class imbalance affected Random Forest performance, we also fitted a balanced version of the model. In this version, each tree used equal numbers of presence and background records. We then compared the balanced and unbalanced models using random cross-validation. MaxEnt settings were optimised separately for each species using ENMeval v.2.0.5 (Kass et al. 2021). We tested four feature-class combinations (L, LQ, LQH, and LQHP) and five regularisation multipliers (0.5, 1, 2, 3, and 4). The final models used LQHP features. Although AICc-based tuning selected RM = 0.5 as the best setting, the R package sdm did not pass the betamultiplier argument to MaxEnt. Consequently, both species were modelled using the default RM value of 1. Model performance was measured using ten-fold random cross-validation and five-fold spatial block cross-validation implemented in the R package blockCV v.3.2-0 (Roberts et al. 2017; Valavi et al. 2019). The main spatial evaluation used 300-km blocks, and we also tested 150- and 500-km blocks to assess sensitivity to block size. Predictive performance was measured using the area under the receiver operating characteristic curve (AUC) and the True Skill Statistic (TSS). We also compared the default Random Forest model with a downsampled version to check whether the imbalance between presence and background records affected model performance. Ensemble predictions were produced by weighting the individual algorithms according to their TSS values. Continuous suitability predictions were converted to binary maps using the threshold that maximised the sum of sensitivity and specificity (Allouche et al. 2006). We then projected the fitted models onto the Last Interglacial (LIG; ca 130 ka) and Last Glacial Maximum (LGM; ca 21 ka) climate conditions.

We evaluated environmental novelty in palaeoclimatic projections using Multivariate Environmental Similarity Surface (MESS) analyses (Elith et al. 2010). We generated MESS surfaces using the R package dismo v.1.3-16 (Hijmans et al. 2017) and used them to identify cells with environmental conditions outside the calibration range. Cells with negative MESS values were excluded from subsequent analyses. For broad-scale comparisons, the filtered continuous ensemble predictions were converted into binary suitability maps using the maximum sensitivity plus specificity threshold. These maps were used to distinguish areas predicted as suitable only for *C. albidus*, only for *C. creticus*, or for both species during the LIG and LGM.

We mapped the spatial overlap between the predicted distributions of the two species for each period using four classes: unsuitable for both species, suitable only for *C. albidus*, suitable only for *C. creticus*, and suitable for both species. For the LGM and LIG, we used MESS-masked binary suitability maps to ensure that overlap classes excluded extrapolated predictions. We then calculated the area of each class in square kilometres for each period. We performed all spatial analyses using the R package terra v.1.8-60 (Hijmans et al. 2026). We produced all spatial visualisations and final maps in QGIS v.3.18.2 (QGIS Development Team 2026), using georeferenced raster and vector layers derived from SDM outputs and MESS-filtered suitability maps.

Niche overlap and niche dynamics

We measured climatic niche overlap using the R package ecospat v.4.1.2 (Di Cola et al. 2017). We defined the environmental space using the selected bioclimatic variables and projected both species occurrences and background climatic conditions into this PCA-based space. We used a PCA-based environmental ordination approach and calculated Schoener's D and Warren's I indices, as well as niche-dynamics statistics such as stability, expansion, and unfilling. Because the two species are largely allopatric, we defined species-specific accessible areas (M) as 300-km buffers around occurrence records. Niche equivalency and bidirectional similarity tests were run with 1,000 randomisations using Schoener's D and Warren's I (Warren et al. 2008; Broennimann et al. 2012). Sensitivity to the definition of M was assessed using 200-, 300-, and 500-km buffers.

Haplotype network reconstruction

We obtained 123 cpDNA *trnL–trnF* sequences for *C. albidus* and *C. creticus* from GenBank (Benson et al. 2013). Before analysis, we standardised the sequence headers by correcting one accession-formatting error and three country-name inconsistencies. The sequences were aligned with ClustalW, and haplotypes were identified from the alignment using pegas::haplotype() with its default settings (Thompson et al. 1994). Terminal gaps were treated as unknown nucleotides, whereas internal gaps were retained as alignment differences and were not recoded as separate evolutionary events. We then reconstructed the statistical parsimony network with the haploNet() function in the R package pegas v.1.3. GenBank accession numbers are provided in Suppl. material 2.

Genetic structure using AMOVA

We evaluated genetic differentiation between the two species using Analysis of Molecular Variance (AMOVA)

Table 1. Predictive performance of the four modelling algorithms under random and 300-km spatial cross-validation. AUC, area under the receiver operating characteristic curve; TSS, True Skill Statistic; SD, standard deviation; RF, Random Forest; GLM, Generalised Linear Model; BRT, Boosted Regression Trees.

Species	Algorithm	Random AUC	Random AUC SD	Spatial AUC	Spatial AUC SD	AUC drop	Random TSS	Random TSS SD	Spatial TSS	Spatial TSS SD	TSS drop
Cistus albidus	RF	0.9647	0.0033	0.9312	0.0210	0.0335	0.8636	0.0169	0.7694	0.0538	0.0943
Cistus albidus	MaxEnt	0.9391	0.0049	0.9153	0.0178	0.0238	0.7915	0.0102	0.7606	0.0696	0.0308
Cistus albidus	BRT	0.9315	0.0062	0.9024	0.0193	0.0291	0.7742	0.0177	0.7469	0.0697	0.0273
Cistus albidus	GLM	0.8522	0.0116	0.8364	0.0269	0.0158	0.6405	0.0201	0.6053	0.0791	0.0352
Cistus creticus	RF	0.9653	0.0029	0.9442	0.0169	0.0211	0.8615	0.0190	0.7994	0.0456	0.0621
Cistus creticus	MaxEnt	0.9503	0.0045	0.9392	0.0241	0.0111	0.8161	0.0132	0.7762	0.0672	0.0399
Cistus creticus	BRT	0.9338	0.0095	0.9112	0.0286	0.0226	0.7634	0.0261	0.7095	0.0787	0.0539
Cistus creticus	GLM	0.9129	0.0094	0.9068	0.0334	0.0061	0.6846	0.0252	0.6850	0.0778	−0.0004

in the R package pegas (Paradis et al. 2025), using raw pairwise nucleotide distances and 1,000 permutations, with samples grouped by species identity. We performed all analyses using the R packages msa v.1.40.0, Biostrings v.2.76.0, ape v.5.8-1, and pegas (Bodenhofer et al. 2015; Paradis and Schliep 2019; Pagès et al. 2023; Paradis et al. 2025).

RESULTS

Spatial dynamics of present and palaeo-potential distributions of two *Cistus* species

Species distribution models showed clear spatial differences between *Cistus creticus* and *Cistus albidus* under both current and palaeoclimatic conditions (Figs 1–3). Model performance under spatial cross-validation was generally high but varied among algorithms (Table 1). Random Forest showed the highest performance for both species, with AUC and TSS values of 0.931 and 0.769 for *C. albidus* and 0.944 and 0.799 for *C. creticus*, respectively. MaxEnt also performed strongly, with AUC and TSS values of 0.915 and 0.761 for *C. albidus* and 0.939 and 0.776 for *C. creticus*, respectively. BRT showed intermediate performance, whereas GLM recorded the lowest values, particularly for *C. albidus*. Final suitability maps were derived from TSS-weighted ensemble predictions rather than from a single algorithm. Downsampling had little effect on Random Forest performance for either species, with only small decreases in AUC and TSS compared to the original models (Suppl. material 1: table S7).

Current species distribution models revealed a clear west–east spatial pattern between the two taxa. *C. albidus* predominantly occupied the western Mediterranean, with suitable habitats concentrated in the Iberian Peninsula and southern France. In contrast, *C. creticus* was mainly distributed across the central and eastern Mediterranean regions. The relative importance of climatic predictors differed between the two species, with temperature seasonality (BIO4) dominating the model for *C. albidus* and precipitation of the coldest quarter (BIO19) and isothermality (BIO3) being most important for *C. creticus* (Table 2).

Palaeoclimatic projections, after masking areas with negative MESS values, indicated clear differences in the distribution of climatically suitable areas between the LGM and LIG. During the LGM, suitable areas for *C.*

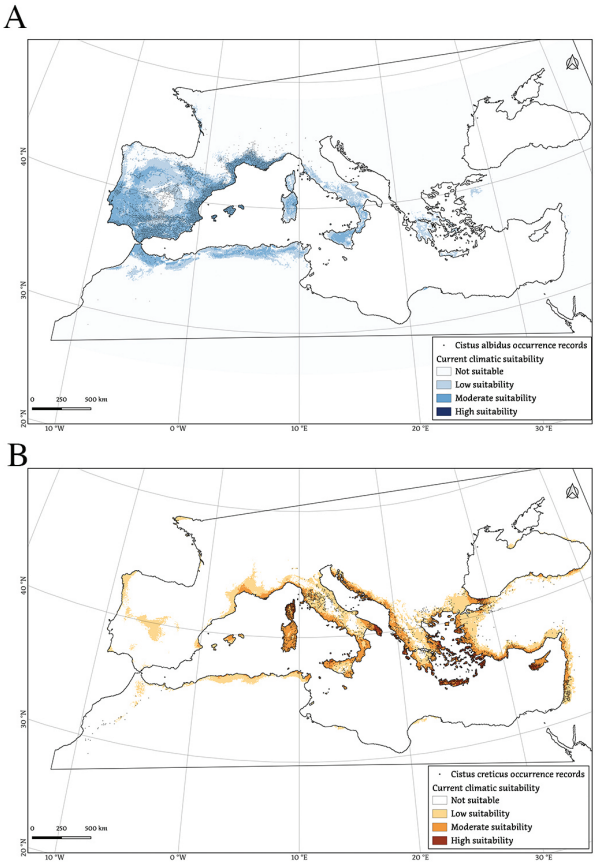

Figure 1. Current climatic suitability based on ensemble species distribution models. **A**. *Cistus albidus*. **B**. *Cistus creticus*. Occurrence records are shown together with predicted suitability classes. Map projection: European Terrestrial Reference System 1989 – Lambert Azimuthal Equal-Area (ETRS89-LAEA).

Table 2. Relative importance of the retained bioclimatic predictors in the True Skill Statistic (TSS)-weighted ensemble models for *Cistus albidus* and *C. creticus*.

Species	Rank	Variable	Description	Weighted importance (%)
C. albidus	1	BIO4	Temperature seasonality	51.57
C. albidus	2	BIO14	Precipitation of the driest month	23.28
C. albidus	3	BIO1	Annual mean temperature	15.09
C. albidus	4	BIO3	Isothermality	6.15
C. albidus	5	BIO19	Precipitation of the coldest quarter	3.91
C. creticus	1	BIO19	Precipitation of the coldest quarter	38.59
C. creticus	2	BIO3	Isothermality	32.36
C. creticus	3	BIO4	Temperature seasonality	13.75
C. creticus	4	BIO1	Annual mean temperature	8.74
C. creticus	5	BIO14	Precipitation of the driest month	6.55

albidus were centred mainly on Italy, with narrower areas along the North African coast and in southern Spain (Fig. 2A–B). In contrast, *C. creticus* showed potential suitability in western Anatolia, along the Greek coasts, on the southern coasts of Italy, in Sardinia, and around the Strait of Gibraltar. During the LIG, suitable areas for *C. albidus* were restricted mainly to western Portugal, the Atlantic coast of France, and parts of Morocco (Fig. 2C–D). *Cistus creticus* retained a more fragmented distribution, with suitable areas around Gibraltar, in Sardinia, southern Italy, Crete and the southern Aegean islands, southern Cyprus, the Levant, and narrow parts of North Africa.

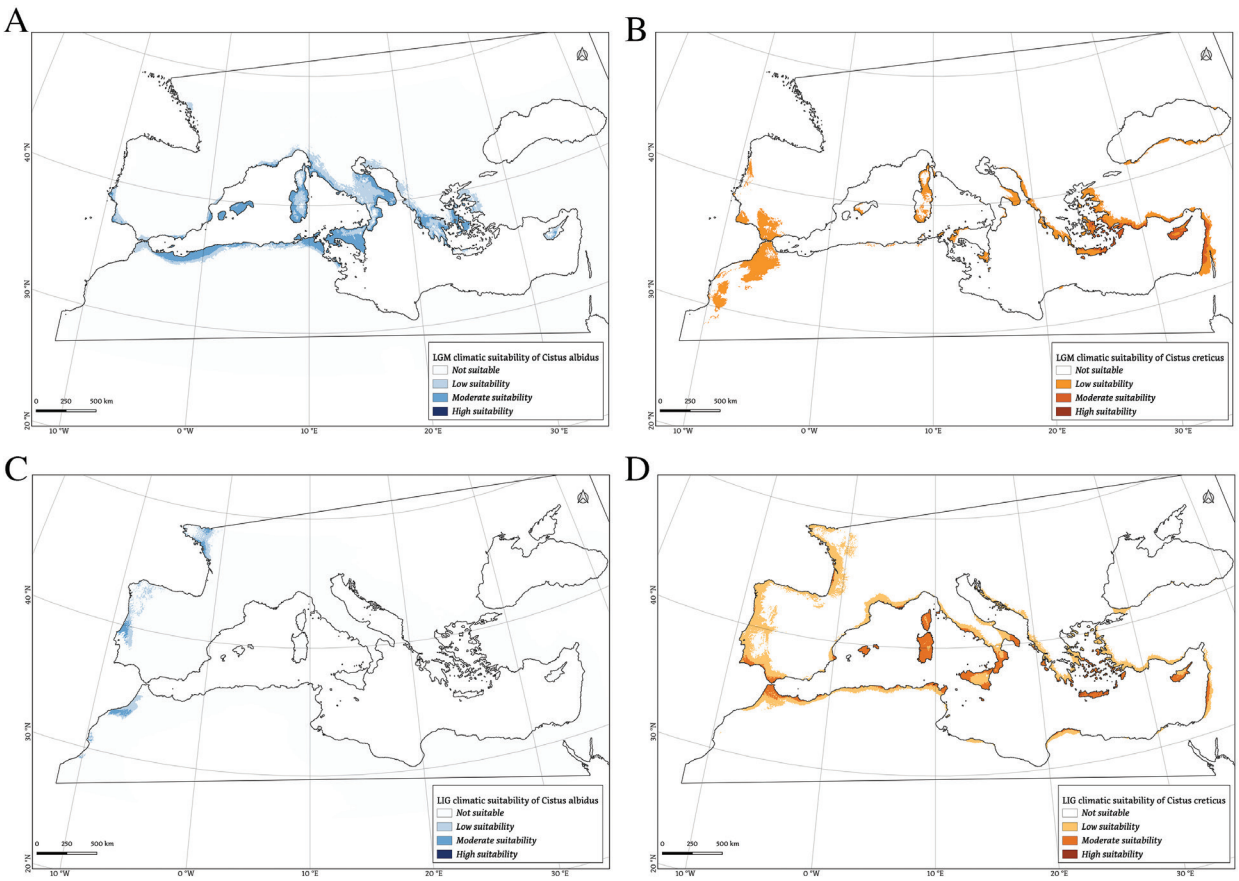

Figure 2. Predicted palaeoclimatic suitability based on True Skill Statistic (TSS)-thresholded ensemble species distribution models. **A**. *Cistus albidus* during the Last Glacial Maximum (LGM). **B**. *Cistus creticus* during the LGM. **C**. *Cistus albidus* during the Last Interglacial (LIG). **D**. *Cistus creticus* during the LIG. Maps show predicted climatic suitability after excluding cells with environmental conditions outside the calibration range. Map projection: European Terrestrial Reference System 1989 – Lambert Azimuthal Equal-Area (ETRS89-LAEA).

Table 3. Climatic niche overlap and hypothesis-testing results between *Cistus albidus* and *C. creticus*.

Observed niche overlap	**Metric**	**Value**
	Schoener's D	0.451
	Warren's I	0.695
Equivalency test	**Metric**	**p value**
	Schoener's D	0.001
	Warren's I	0.001
Similarity tests	**Metric**	**p value**
C. albidus → *C. creticus*	Schoener's D	0.062
C. albidus → *C. creticus*	Warren's I	0.048
C. creticus → *C. albidus*	Schoener's D	0.083
C. creticus → *C. albidus*	Warren's I	0.060

Potential refugial patterns and spatial overlap

The MESS-masked overlap maps showed that the two species shared suitable areas in several parts of the Mediterranean, but the pattern differed between the LGM and LIG. During the LGM, overlap occurred around the Strait of Gibraltar and southwestern Spain, as well as in Sardinia, western Greece, western Anatolia, southern Italy, western Sicily, and Cyprus. During the LIG, shared suitable areas were more limited and were concentrated mainly along the Atlantic coast of France, in Portugal, and in Morocco. Based on the MESS-masked maps, shared suitable areas were more extensive during the LGM, covering 119,971 km² (1.45% of the analysed area), compared with 43,914 km² (0.92%) during the LIG (Fig. 3).

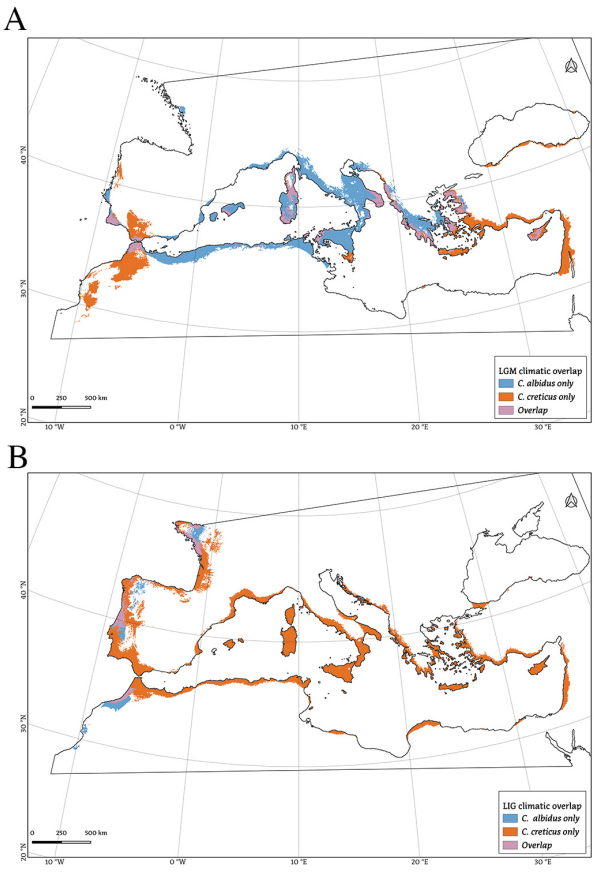

Figure 3. Spatial overlap of binary climatic suitability for *Cistus albidus* and *C. creticus*. **A**. Last Glacial Maximum (LGM). **B**. Last Interglacial (LIG). Areas suitable only for *C. albidus*, only for *C. creticus*, or for both species were derived from binary ensemble predictions filtered using the Multivariate Environmental Similarity Surface (MESS). Map projection: European Terrestrial Reference System 1989 – Lambert Azimuthal Equal-Area (ETRS89-LAEA).

Climatic niche overlap and niche dynamics

PCA-env analysis showed a moderate level of climatic niche overlap between *C. albidus* and *C. creticus* (Schoener's D = 0.451; Warren's I = 0.695; Table 3). Both species occupied broadly stable climatic space, with only restricted expansion and unfilling. The equivalency test showed that their niches were not equivalent (p = 0.001). For Schoener's D, the two directional similarity tests came close to, but did not reach, statistical significance (*C. albidus* fixed: p = 0.062; *C. creticus* fixed: p = 0.083). Results based on Warren's I were mixed (p = 0.048 and p = 0.060, respectively). This suggests that the niches may have become more similar, although the evidence was too weak to support a firm conclusion (Fig. 4A–B).

Genetic structure and haplotype network

Analysis of molecular variance (AMOVA) revealed significant genetic differentiation between *C. albidus* and *C. creticus* ($p < 0.001$; Table 4). However, the two species were not completely separated because they shared the most common haplotype. We identified seven haplotypes in total, with haplotype IV being the most frequent in both species. The other haplotypes were less common and were mostly found in only one species (Fig. 4C).

DISCUSSION

Our results reveal a broad biogeographic pattern linking the distributions and climatic niches of *C. albidus* and

Table 4. Analysis of molecular variance (AMOVA) for genetic differentiation between *Cistus albidus* and *C. creticus*.

Source of variation	d.f.	SSD	MSD	p value
Between species	1	0.000635	0.000635	< 0.001
Within species	121	0.003584	0.0000296	—
Total	122	0.004219	0.0000346	—

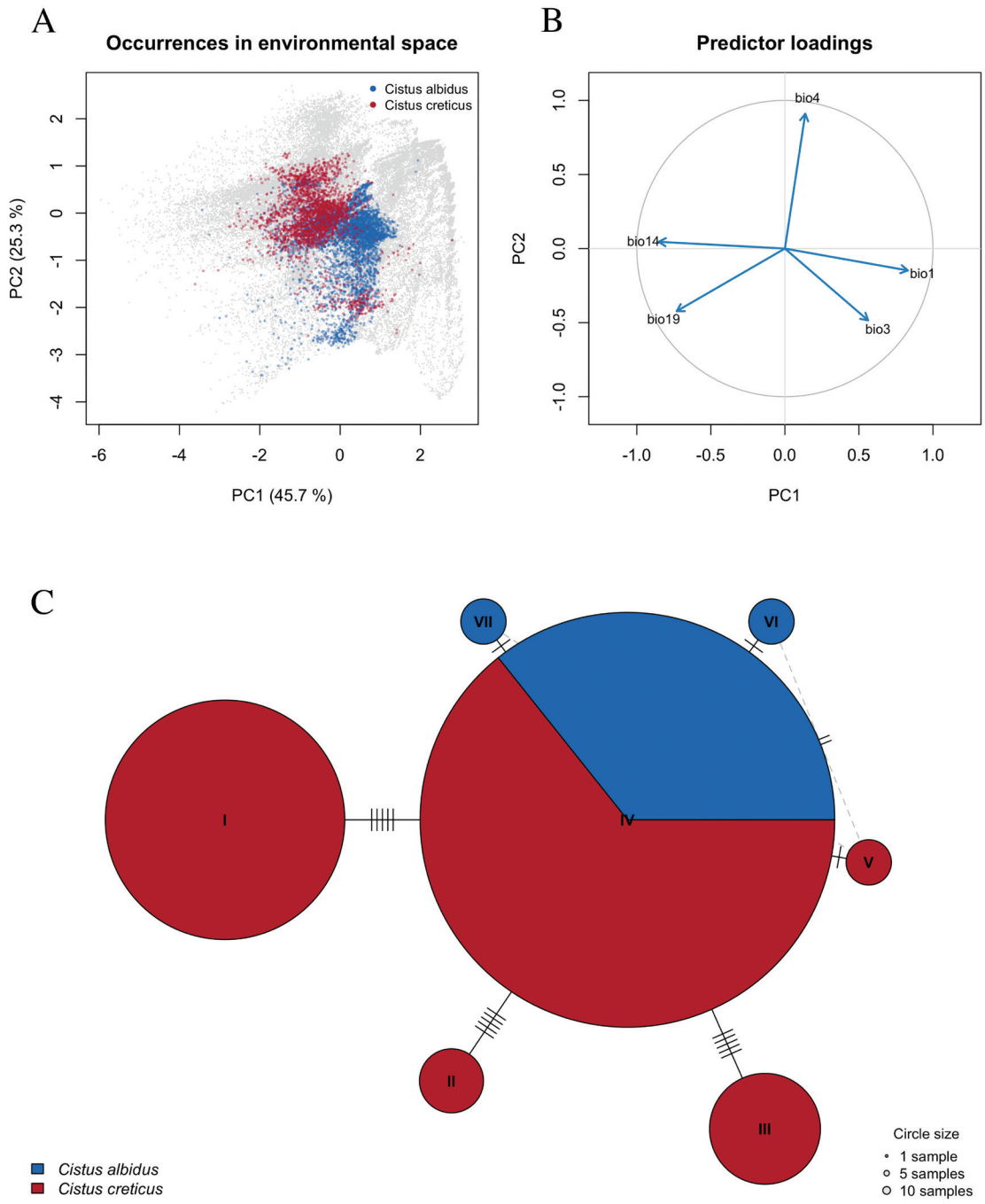

Figure 4. Climatic niche structure and chloroplast DNA (cpDNA) haplotype relationships of *Cistus albidus* and *C. creticus*. **A–B**. Occurrence patterns and predictor loadings in principal component analysis of environmental space (PCA-env). **C**. Statistical parsimony network of *trnL–trnF* haplotypes; node size reflects haplotype frequency, colours indicate species identity, and short bars represent mutational steps.

C. creticus, together with partial genetic differentiation between them. Species distribution patterns show a clear west–east division across the Mediterranean Basin, with *C. albidus* primarily associated with the western Mediterranean and *C. creticus* distributed across central and eastern regions. Although several factors influence species distributions, climate is generally considered the primary driver and the most commonly used predictor in species distribution modelling (Hua and Wiens 2013). However, species distributions may also be constrained by historical factors and dispersal limitations rather than equilibrium with current climate (Svenning and Skov 2007).

A key question is whether this west–east separation reflects climatic niche divergence or historical geographic isolation. Climatic niche divergence may promote speciation as populations adapt to different environmental conditions, whereas niche conservatism may allow geographic isolation to develop without major ecological differentiation (Rundle and Nosil 2005; Schluter 2009; Wiens 2016). Our climatic niche analyses indicate partial overlap rather than complete niche divergence. The two species showed moderate climatic niche overlap (Schoener's D = 0.451; Warren's I = 0.695), together with high niche stability in both directions (0.959 and 0.946) and low expansion and unfilling values (0.041–0.054). For Schoener's D, the directional similarity tests were not significant, although the p values were fairly low (*C. albidus* fixed: p = 0.062; *C. creticus* fixed: p = 0.083), while Warren's I gave mixed results (p = 0.048 and 0.060, respectively). This suggests some niche similarity, although the evidence was not strong enough to conclude that the observed overlap exceeded what would be expected by chance. Overall, the two species appear to occupy broadly similar climatic conditions, although their niches are not fully equivalent. Climatic niche divergence therefore seems unlikely to be the primary explanation for their present geographic separation. This pattern is also consistent with the broader biogeographic history of the Mediterranean Basin, where geological, tectonic, and climatic processes have frequently contributed to east–west lineage differentiation (Thompson 2020). Similar separation patterns are well known in Mediterranean plants such as *Arbutus* L., *Juniperus* L., and *Astragalus* L., demonstrating how geographic isolation has shaped biodiversity in the region over time (Grivet et al. 2009; Feliner 2014; Hardion et al. 2016).

The central Mediterranean, particularly the Italian Peninsula and adjacent marine systems, likely served as both a corridor and a barrier (Thompson 2020). Mountain ranges such as the Alps and Apennines, with marine barriers including the Tyrrhenian and Adriatic Seas, may have inhibited dispersal and limited gene flow between western and eastern populations, thus reinforcing lineage separation (Médail and Diadema 2009; Feliner 2014). Potential refugial dynamics may also have played a role in this process. During repeated Pleistocene climate changes, suitable habitats were fragmented into isolated refugial areas across the Mediterranean Basin (Médail and Diadema 2009). Previous phylogeographic work suggested a complicated evolutionary history for *C. creticus*, with two genetically distinct lineages: an Eastern Mediterranean clade retaining more ancestral characteristics and a more heterogeneous Western Mediterranean clade. The same study also reported a shared ancestral chloroplast haplotype between *C. albidus* and the Eastern Mediterranean lineage of *C. creticus* (Lukas et al. 2021). Our palaeoclimatic projections provide independent ecological and spatial support for a geographic separation between the western and eastern parts of the species' ranges. They also show that similar climatic niches do not necessarily result in complete geographic coexistence, although the species' suitable ranges overlapped to some extent during the LGM. The location of suitable climates changed through time, with less overlap during the LIG and a wider, though still limited, pattern of shared suitability during the LGM. At the same time, the genetic results do not suggest complete lineage separation. The widespread occurrence of the dominant haplotype suggests that both species may have retained ancestral plastid variation, possibly because lineage sorting remains incomplete after a relatively recent divergence. Overall, the current west–east pattern is more consistent with historical geographic isolation and uneven range shifts than with strong climatic niche divergence. However, it should not be interpreted as evidence of complete genetic isolation or strictly allopatric speciation.

Although ecological differences between the two species may contribute to maintaining their current distributions, these differences likely occur at local scales. *C. albidus* occupies a broader altitudinal range and more heterogeneous habitats, whereas *C. creticus* is more closely associated with open, dry Mediterranean environments such as maquis vegetation (Guzmán and Vargas 2010). These ecological differences are consistent with the partial niche overlap observed in our analyses and suggest that small-scale habitat variation may also contribute to their current distributions.

Phylogenetic studies of Mediterranean *Cistus* indicate that diversification within the genus has followed different evolutionary pathways. In the white-flowered lineage, environmental heterogeneity and the evolution of contrasting leaf traits have been linked to adaptive radiation (Guzmán et al. 2009). In contrast, our results for the purple-flowered *C. albidus* and *C. creticus* suggest that geographic isolation and Pleistocene range dynamics played a greater role than strong climatic niche divergence. More broadly, patterns observed within individual species and across different regions show that the mechanisms driving divergence are not always the same. *Cistus monspeliensis* L., for example, shows refugial persistence and postglacial expansion in the Mediterranean, together with repeated inter-island colonisation and high plastid diversity in the Canary Islands (Fernández-Mazuecos and Vargas 2011; Coello et al. 2021). Comparative studies also show that habitat specificity and elevation can influence

genetic structure as well as geographic distance and marine barriers (Fernández-Mazuecos and Vargas 2010). In summary, these studies indicate that diversification in *Cistus* reflects varying combinations of ecological differentiation, geographic isolation, and historical range change. Within this framework, the present west–east separation of *C. albidus* and *C. creticus* is better explained by historical geographic isolation and potential refugial patterns than by strong differentiation in their broad climatic niches.

CONCLUSION

Our species distribution models and climatic niche analyses suggest that the present-day west–east separation of *C. albidus* and *C. creticus* is not mainly the result of strong climatic niche differences. Instead, their distributions appear to have been shaped by geographic separation during the Pleistocene and by limited dispersal across the Mediterranean Basin. The genetic results suggest a more recent and incomplete divergence, since the species differ significantly but continue to share the dominant haplotype. Overall, the results show how historical range changes, geographic barriers, and incomplete lineage sorting can jointly shape diversification in Mediterranean plants.

DATA AVAILABILITY STATEMENT

The cleaned occurrence data, R scripts, and derived tabular outputs used in this study are available on Zenodo: https://doi.org/10.5281/zenodo.20358283.

GenBank accession numbers are provided in Suppl. material 2.

ACKNOWLEDGEMENTS

The author received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors and declares no conflict of interest.

REFERENCES

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38: 541–545. https://doi.org/10.1111/ecog.01132

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Barbero M, Lebreton P, Quézel P (1994) Sur les affinités biosystématiques et phytoécologiques de *Juniperus thurifera* L. et de *Juniperus excelsa* Bieb. Ecologia Mediterranea 20(3): 21–37. https://doi.org/10.3406/ecmed.1994.1739

Barbéro M, Loisel R, Quézel P, Richardson DM, Romane F (1998) Pines of the Mediterranean Basin. In: Richardson DM (Ed.) Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, 153–170.

Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2013) GenBank. Nucleic Acids Research 41: D36–D42. https://doi.org/10.1093/nar/gks1195

Bodenhofer U, Bonatesta E, Horejš-Kainrath C, Hochreiter S (2015) msa: an R package for multiple sequence alignment. Bioinformatics 31: 3997–3999. https://doi.org/10.1093/bioinformatics/btv494

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M, Randin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21: 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Brown JL, Hill DJ, Dolan AM, Carnaval AC, Haywood AM (2018) PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. Scientific Data 5: 180254. https://doi.org/10.1038/sdata.2018.254

Civeyrel L, Leclercq J, Demoly J-P, Agnan Y, Quèbre N, Pélissier C, Otto T (2011) Molecular systematics, character evolution, and pollen morphology of *Cistus* and *Halimium* (Cistaceae). Plant Systematics and Evolution 295: 23–54. https://doi.org/10.1007/s00606-011-0458-7

Coello AJ, Fernández-Mazuecos M, García-Verdugo C, Vargas P (2021) Phylogeographic sampling guided by species distribution modeling reveals the Quaternary history of the Mediterranean–Canarian *Cistus monspeliensis* (Cistaceae). Journal of Systematics and Evolution 59: 262–277. https://doi.org/10.1111/jse.12570

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, d'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40: 774–787. https://doi.org/10.1111/ecog.02671

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Feliner GN (2014) Patterns and processes in plant phylogeography in the Mediterranean Basin. A review. Perspectives in Plant Ecology, Evolution and Systematics 16: 265–278. https://doi.org/10.1016/j.ppees.2014.07.002

Fernández-Mazuecos M, Vargas P (2010) Ecological rather than geographical isolation dominates Quaternary formation of Mediterranean *Cistus* species. Molecular Ecology 19: 1381–1395. https://doi.org/10.1111/j.1365-294X.2010.04549.x

Fernández-Mazuecos M, Vargas P (2011) Genetically depauperate in the continent but rich in oceanic islands: *Cistus monspeliensis* (Cistaceae) in the Canary Islands. PLoS ONE 6: e17172. https://doi.org/10.1371/journal.pone.0017172

Fitzpatrick BM, Fordyce JA, Gavrilets S (2009) Pattern, process and geographic modes of speciation. Journal of Evolutionary Biology 22: 2342–2347. https://doi.org/10.1111/j.1420-9101.2009.01833.x

GBIF (2025a) GBIF occurrence download. https://doi.org/10.15468/dl.wsvrh2 [accessed 03.05.2025].

GBIF (2025b) GBIF occurrence download. https://doi.org/10.15468/dl.rwwp5t [accessed 03.05.2025].

Grivet D, Sebastiani F, González-Martínez SC, Vendramin GG (2009) Patterns of polymorphism resulting from long-range colonization in the Mediterranean conifer Aleppo pine. New Phytologist 184: 1016–1028. https://doi.org/10.1111/j.1469-8137.2009.03015.x

Guzmán B, Vargas P (2005) Systematics, character evolution, and biogeography of *Cistus* L. (Cistaceae) based on ITS, *trnL-trnF*, and *matK* sequences. Molecular Phylogenetics and Evolution 37: 644–660. https://doi.org/10.1016/j.ympev.2005.04.026

Guzmán B, Vargas P (2010) Unexpected synchronous differentiation in Mediterranean and Canarian *Cistus* (Cistaceae). Perspectives in Plant Ecology, Evolution and Systematics 12: 163–174. https://doi.org/10.1016/j.ppees.2009.09.002

Guzmán B, Lledó MD, Vargas P (2009) Adaptive radiation in Mediterranean *Cistus* (Cistaceae). PLoS ONE 4: e6362. https://doi.org/10.1371/journal.pone.0006362

Hardion L, Dumas P-J, Abdel-Samad F, Kharrat MBD, Surina B, Affre L, Médail F, Bacchetta G, Baumel A (2016) Geographical isolation caused the diversification of the Mediterranean thorny cushion-like *Astragalus* L. sect. *Tragacantha* DC. (Fabaceae). Molecular Phylogenetics and Evolution 97: 187–195. https://doi.org/10.1016/j.ympev.2016.01.006

Hijmans RJ, Phillips S, Leathwick J, Elith J (2017) dismo: species distribution modelling. http://rspatial.org/sdm/ [accessed 18.07.2026]

Hijmans RJ, Bivand R, Forner K, Ooms J, Pebesma E, Sumner MD (2026) terra: spatial data analysis. https://rspatial.github.io/terra/ [accessed 18.07.2026]

Hua X, Wiens JJ (2013) How does climate influence speciation? The American Naturalist 182: 1–12. https://doi.org/10.1086/670690

Julve P (2018) Listes départementales des plantes de France. Tela Botanica. https://www.tela-botanica.org [accessed 17.07.2026]

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4: 1–20. https://doi.org/10.1038/sdata.2017.122

Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP (2021) ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution 12: 1602–1608. https://doi.org/10.1111/2041-210X.13628

Lukas B, Jovanovic D, Schmiderer C, Kostas S, Kanellis A, Gómez Navarro J, Aytaç Z, Koç A, Sözen E, Novak J (2021) Intraspecific genetic diversity of *Cistus creticus* L. and evolutionary relationships to *Cistus albidus* L. (Cistaceae): meeting of the generations? Plants 10: 1619. https://doi.org/10.3390/plants10081619

Médail F, Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Annals of the Missouri Botanical Garden 84: 112–127. https://doi.org/10.2307/2399957

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. Journal of Biogeography 36: 1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x

Naimi B, Araújo MB (2016) sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39: 368–375. https://doi.org/10.1111/ecog.01881

Pagès H, Aboyoun P, Gentleman R, DebRoy S (2023) Biostrings: Efficient manipulation of biological strings. https://bioconductor.org/packages/Biostrings [accessed 23.07.2026]

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Paradis E, Jombart T, Kamvar ZN, Knaus B, Schliep K, Potts A, Winter D, Paradis ME (2025) pegas: Population and evolutionary genetics analysis system. https://CRAN.R-project.org/package=pegas [accessed 18.07.2026]

POWO (2026) Plants of the World Online. Facilitated by the Royal Botanic Gardens. http://www.plantsoftheworldonline.org [accessed 17.07.2026]

QGIS Development Team (2026) QGIS Geographic Information System. http://www.qgis.org [accessed 18.07.2026]

Rieseberg LH, Willis JH (2007) Plant speciation. Science 317: 910–914. https://doi.org/10.1126/science.1137729

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40: 913–929. https://doi.org/10.1111/ecog.02881

Rundle HD, Nosil P (2005) Ecological speciation. Ecology Letters 8: 336–352. https://doi.org/10.1111/j.1461-0248.2004.00715.x

Schluter D (2009) Evidence for ecological speciation and its alternative. Science 323: 737–741. https://doi.org/10.1126/science.1160006

Società Botanica Italiana (2026) Portale della Flora d'Italia. https://dryades.units.it/floritaly/ [accessed 17.07.2026]

Svenning J, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10: 453–460. https://doi.org/10.1111/j.1461-0248.2007.01038.x

Thompson JD (2020) Plant Evolution in the Mediterranean: Insights for Conservation. Second edition. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780198835141.001.0001

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680. https://doi.org/10.1093/nar/22.22.4673

Thompson JD, Fauché M, Papuga G, Gauthier P (2026) Plant conservation in a changing Mediterranean world. Plants, People, Planet 8: 49–72. https://doi.org/10.1002/ppp3.70036

Turelli M, Barton NH, Coyne JA (2001) Theory and speciation. Trends in Ecology & Evolution 16: 330–343. https://doi.org/10.1016/S0169-5347(01)02177-2

Valavi R, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2019) blockCV: an R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. Methods in Ecology and Evolution 10: 225–232. https://doi.org/10.1111/2041-210X.13107

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58: 193–197. https://doi.org/10.1111/j.0014-3820.2004.tb01586.x

Wiens JJ (2016) Climate-related local extinctions are already widespread among plant and animal species. PLoS Biology 14: e2001104. https://doi.org/10.1371/journal.pbio.2001104

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svantesson S, Wengström N, Zizka V, Antonelli A (2019) CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution 10: 744–751. https://doi.org/10.1111/2041-210X.13152

SUPPLEMENTARY MATERIALS

Supplementary material 1

Occurrence-data cleaning, predictor diagnostics, model tuning, environmental novelty assessment and sensitivity analyses for *Cistus albidus* and *C. creticus*.

https://doi.org/10.5091/plecevo.201010.suppl1

Supplementary material 2

GenBank accession numbers of chloroplast *trnL–trnF* sequences used for haplotype network reconstruction and analysis of molecular variance.

https://doi.org/10.5091/plecevo.201010.suppl2